Bonine I

Phylogenetics (Ch 27)

Thursday
29 January 2009
ECOL 182R UofA
K. E. Bonine

Kevin Bonine, Ph.D.

Tucson ~native

University of Arizona (undergrad)

- Ecology & Evolutionary Biology
- Economics

University of Wisconsin, Madison (graduate)

Zoology, Evolutionary Physiology

Reptiles & Amphibians

Teaching at UA since 2002

Herpetology
Vertebrate Physiology
Conservation Biology
Environmental Biology
Introductory Biology

kebonine"at"u.arizona.edu

M 1:10-2pm
W 11:10-11am
in BSE113

Mostly Middle-Third of this course (plants etc.)

Text readings are highly encouraged

Website: For my lecture material:
http://www.eebweb.arizona.edu/courses/182-spring2009-Bonine/182-BONINE-sp2009.htm

There is a link from Dr. Schaffer's 182R website.

Text: The text is Freeman, Scott. 2008. *Biological Science* (Third Edition). Pearson Benjamin Cummings, San Francisco, CA. Available at UA Bookstore.

Posted Lecture Notes

Items in orange will not be available on-line (except for today), but they will be presented during lecture.

Note that slides are numbered for easy reference.

I will strive to post the lecture PDF file on your D2L site before lecture.

How do we organize/categorize biodiversity? Why would we want to?

Linnaean Taxonomy (1700s)

- **Taxonomy** is the effort to name and classify organisms.
- In Linnaeus' taxonomic system for classifying organisms, each organism is given a unique two-part scientific name consisting of the **genus** and the **species**.

(1) A ***genus*** is made up of a closely related group of species.

(2) A ***species*** is made up of individuals that regularly breed together and/or have characteristics that are distinct from those of other species.

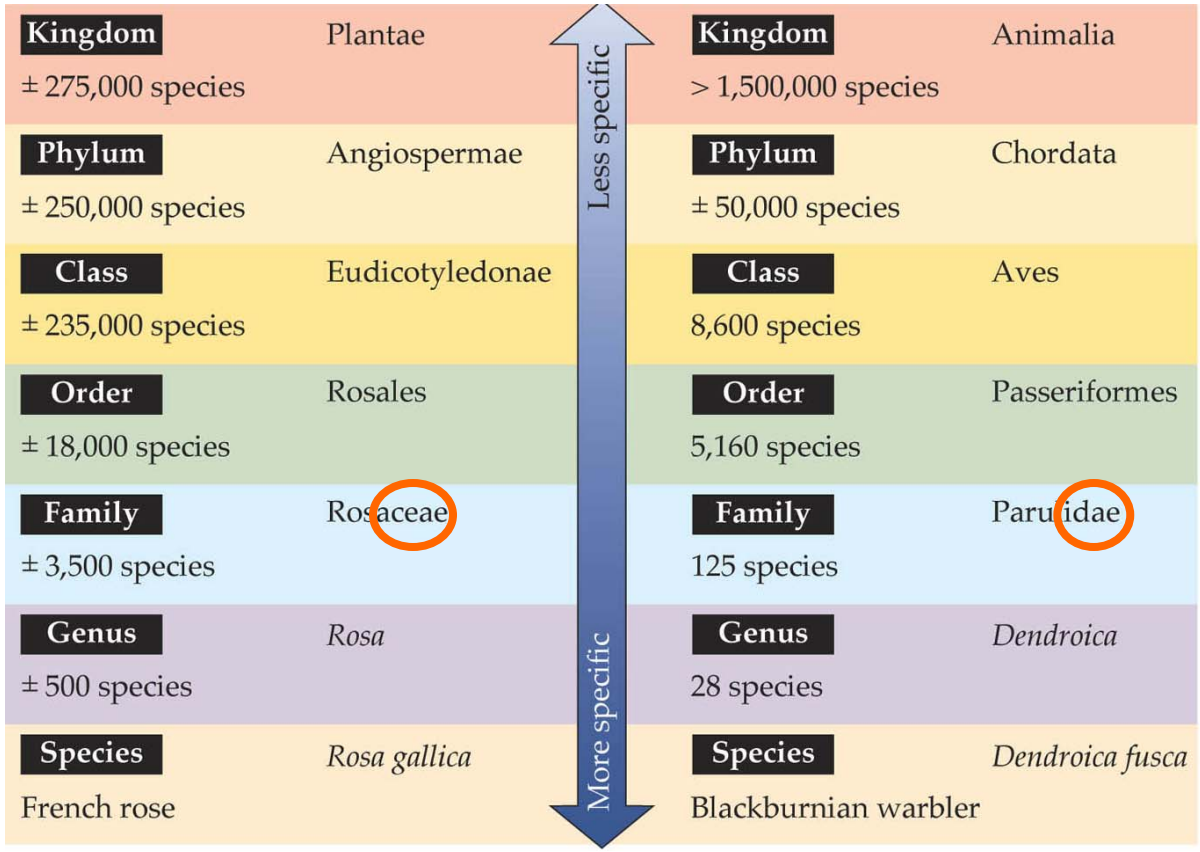
Taxonomic Levels

- Linnaeus' system is hierarchical with nested **taxa**. The taxonomic levels from least to most specific are as follows:

domain
kingdom
phylum
class
order
family
genus
species

Linnaean hierarchy

- Group of organisms treated as unit is a taxon (plural taxa)
- Hierarchy of taxonomic categories



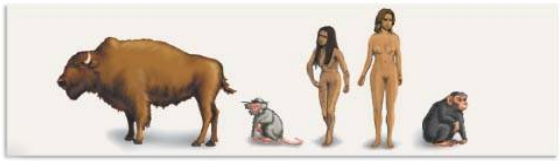
Italics

Linnaeus' Taxonomic Levels

KINGDOM
(Animalia)

PHYLUM
(Chordata)

CLASS
(Mammalia)



ORDER
(Primates)

FAMILY
(Hominidae)

GENUS
(*Homo*)

SPECIES
(*Homo sapiens*)

Theory of common descent

- Any two organisms can trace back to a common ancestor
- We all belong to a big family tree, some more closely related than others
- On the right is a history of individuals: can also draw up the history of species

Phylogeny

- Phylogeny = history of exactly how a group of organisms are descended from their common ancestor

- Phylogenetic tree = representation of that history

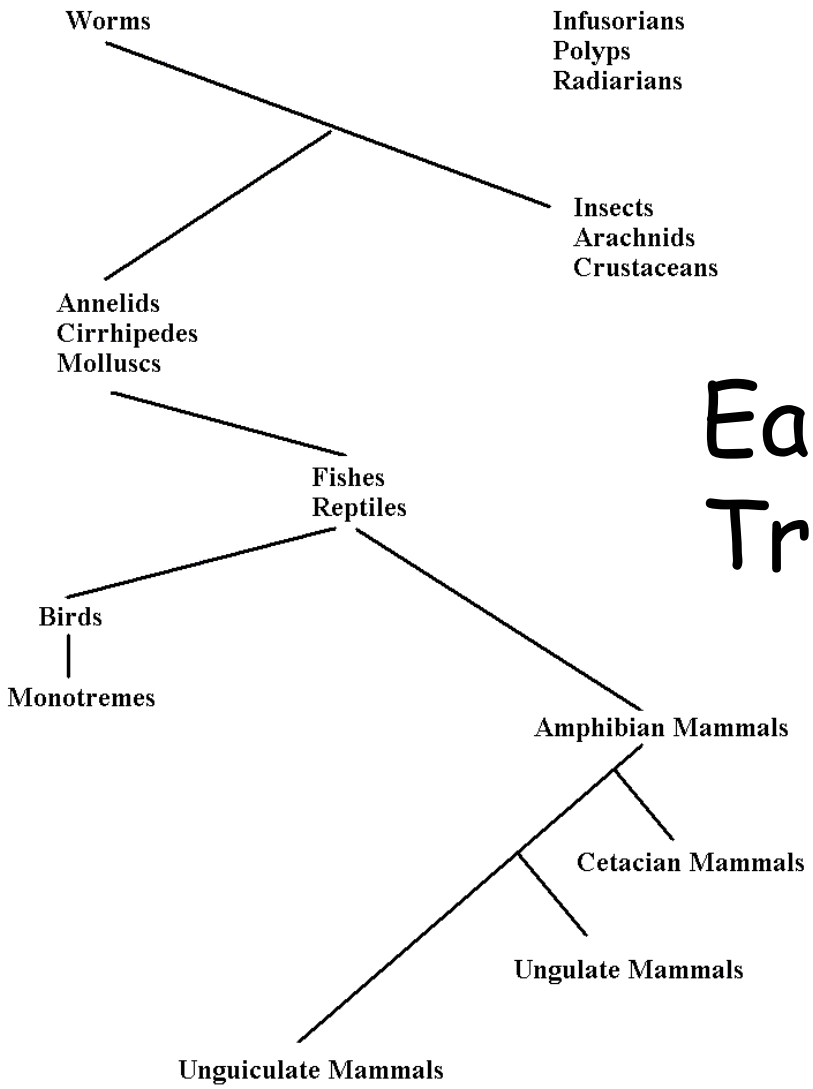
Lamarck

1821. From Desmond 1989, p. 43.

http://www.nceas.ucsb.edu/~alroy/lefa/Lamarck.jpg

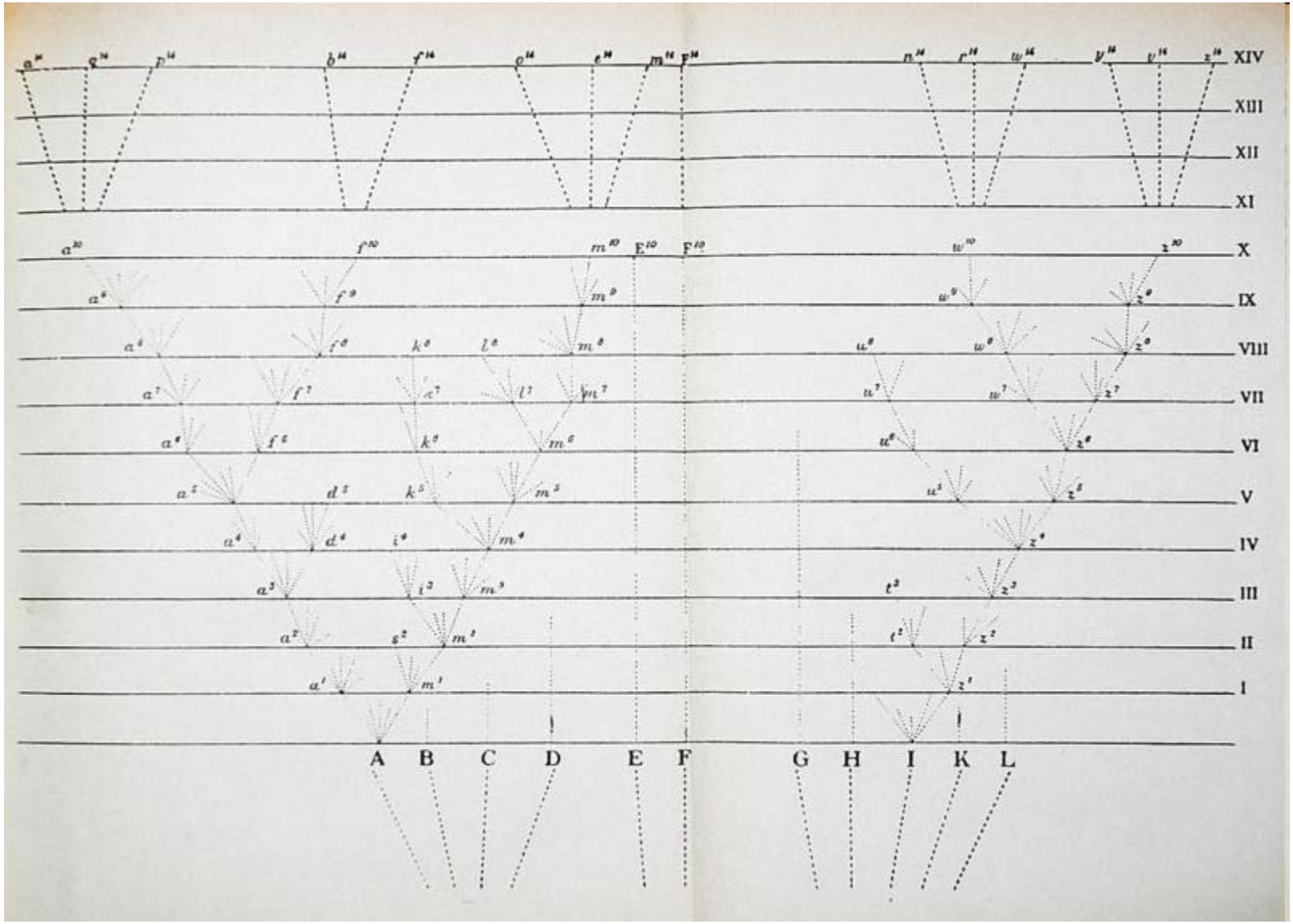
http://www.tulane.edu/~darwin/Herbarium/Herbarium/Koch%20Images/Lamarck2.jpg

"Cineraria"
Jean Baptiste Pierre Antoine de Monet de Lamarck (1744-1829): *Tableau encyclopedique et methodique des trois regnes de la nature... botanique.* Paris, 1791-1823

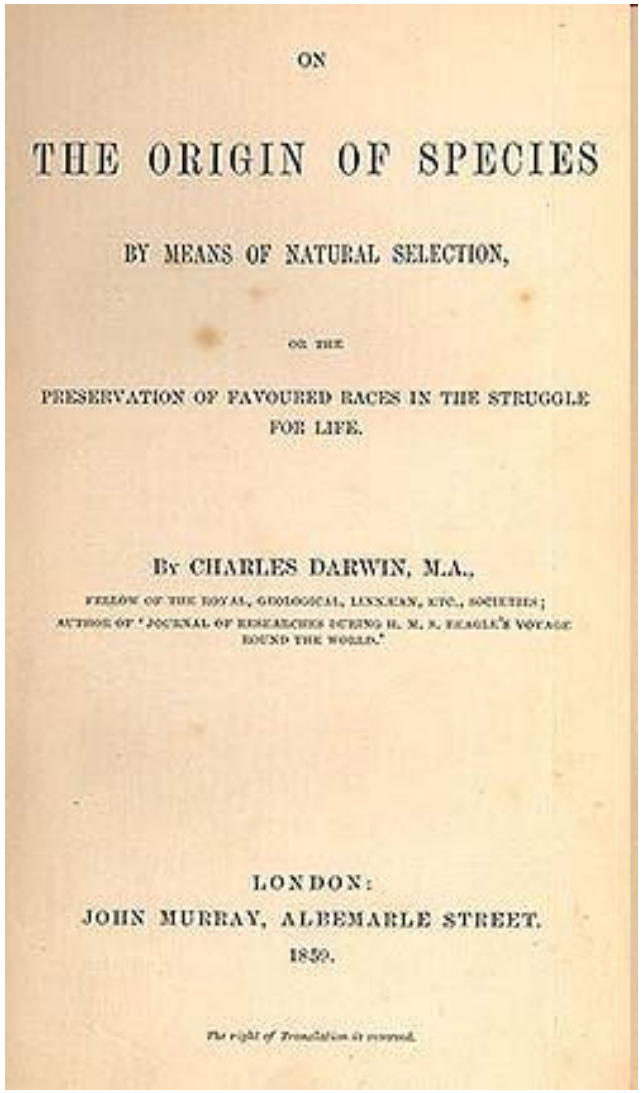


Early Phylogenetic Tree by Lamarck

http://bill.srnr.arizona.edu/classes/182/Zool%20Phil%20Tree%20crop-700.gif



Tree diagram used to show the divergence of species. It is the only illustration in *The Origin of Species* – Darwin 1859.



ON

THE ORIGIN OF SPECIES

BY MEANS OF NATURAL SELECTION,

OR THE

PRESERVATION OF FAVOURED RACES IN THE STRUGGLE FOR LIFE.

By CHARLES DARWIN, M.A.,

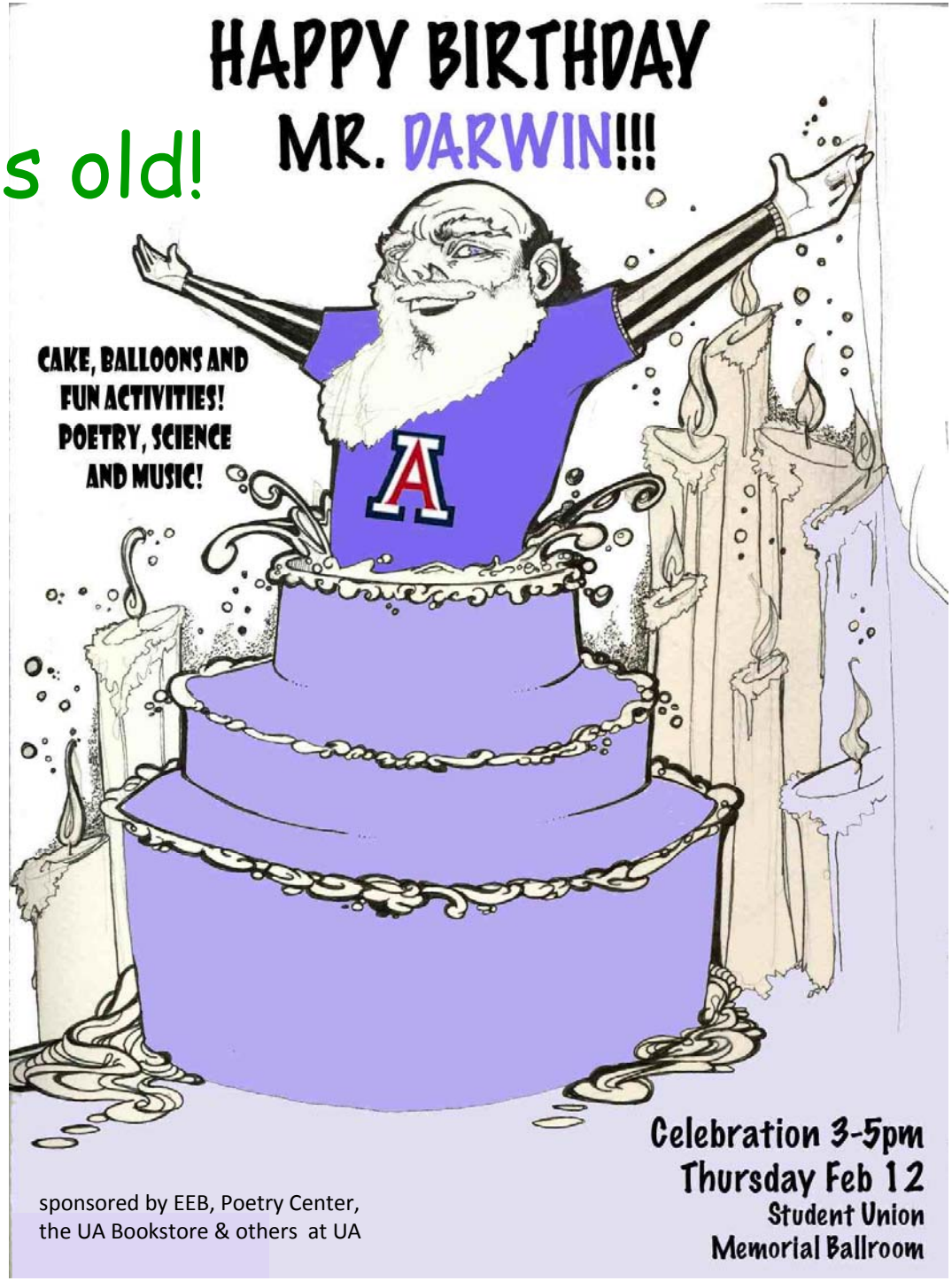
FELLOW OF THE ROYAL, GEOLOGICAL, LINNEAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

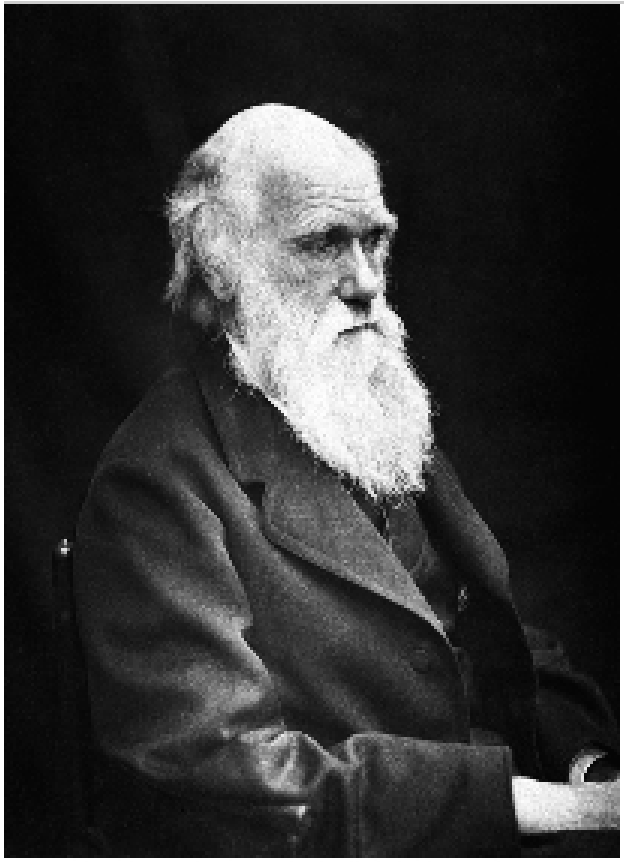
The right of Translation is reserved.

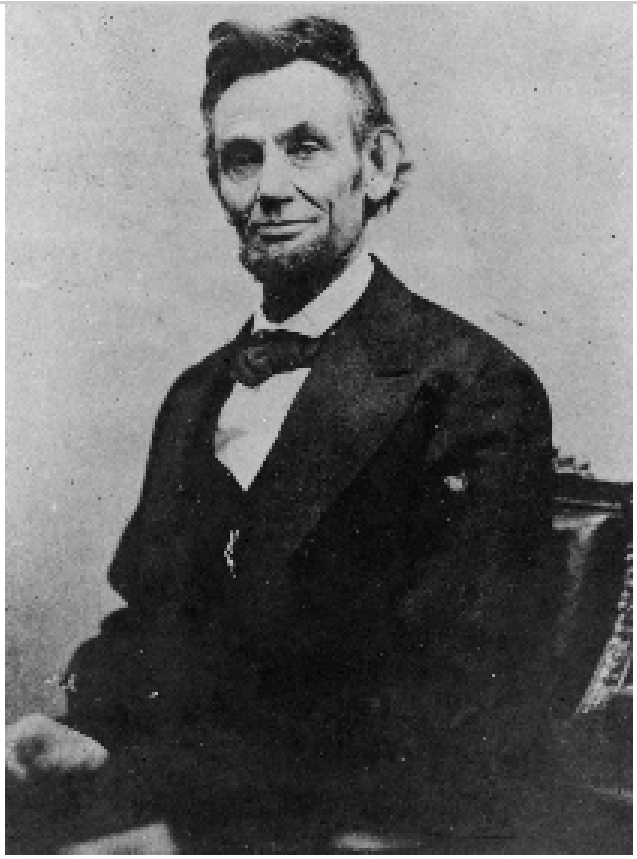
Title page of the 1859 edition of *On the Origin of Species*

200 years old!



12 Feb 2009





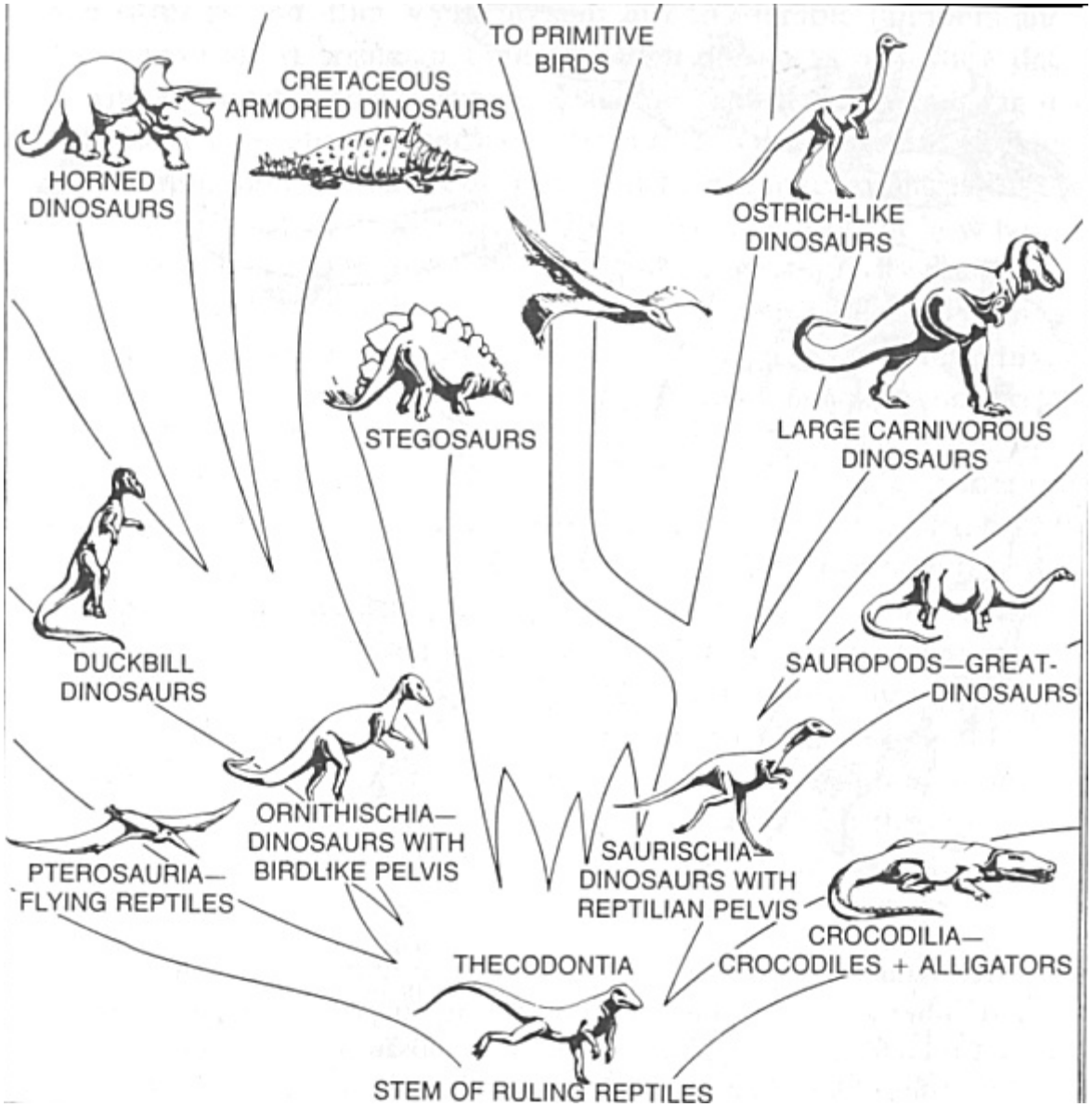
They Still Free Minds and Peoples

Darwin & Lincoln's Birthday, February 12th, 1809

http://media.richarddawkins.net/images/2008/darwinday/016_FrederickBrenion.jpg

- A phylogenetic tree is a graphical representation of the evolutionary relationships among species. Phylogenies can be established by analyzing similarities and differences in traits.

Often we are attempting to identify relationships from the distant past…

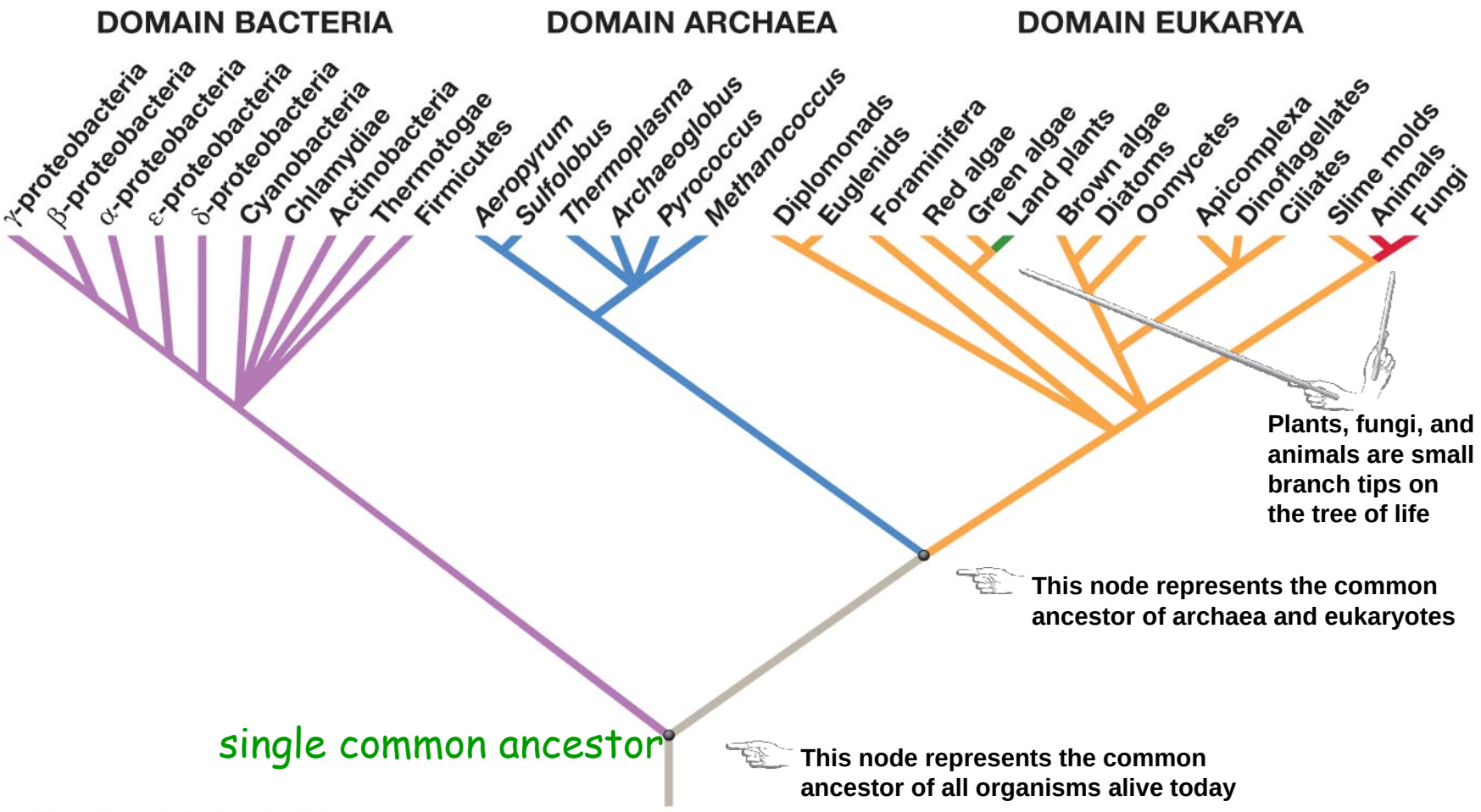


Phylogenetic Trees

- **Systematics**, the study of organismal diversity with respect to evolutionary (or not) relationships between organisms (patterns of descent).
  - **Taxonomy** – a subdiscipline that relates to classification

- What evolutionary relationships could be useful/helpful to understand?

Phylogenetic Tree of Life



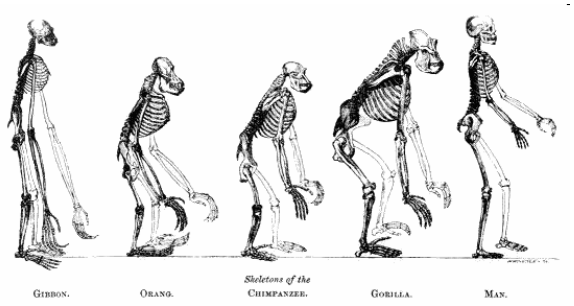
Remember that >99% of all species are EXTINCT!

Old species often become new species…

Darwin's eventual conclusions stemming from his first question about the birds and plants of the Galapagos were to feature in one of the most important passages in *Origin of species* (pp. 397-406). The passage ended with one of his key points about evolution by natural selection:

> The relations just discussed … [including] the very close relation of the distinct species which inhabit the islets of the same archipelago, and especially the striking relation of the inhabitants of each whole archipelago or island to those of the nearest mainland, are, I think, utterly inexplicable on the ordinary view of the independent creation of each species, but are explicable on the view of colonisation from the nearest and readiest source, together with the subsequent modification and better adaptation of the colonists to their new homes.

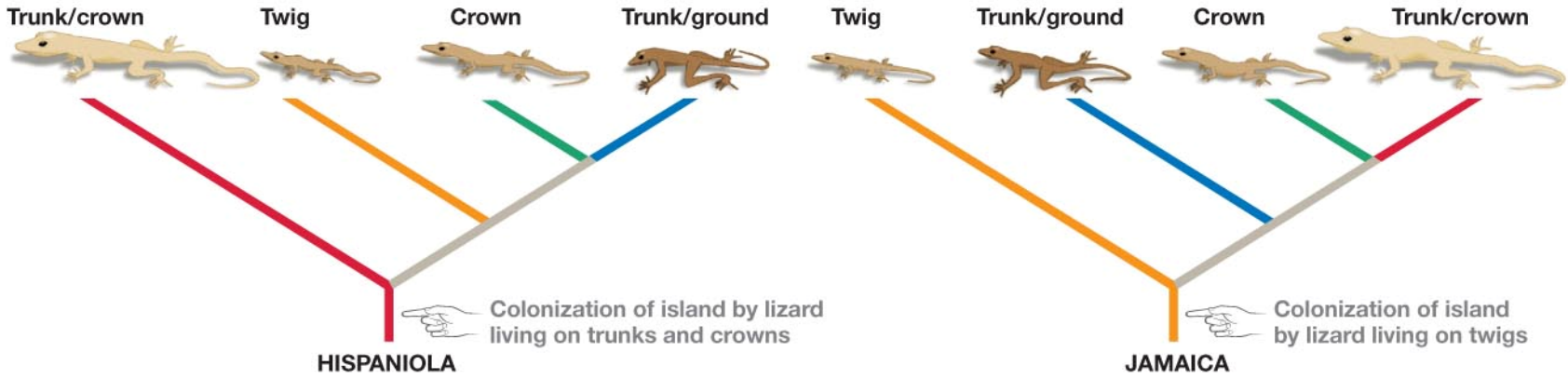
http://darwin-online.org.uk/EditorialIntroductions/Chancellor_Keynes_Galapagos.html



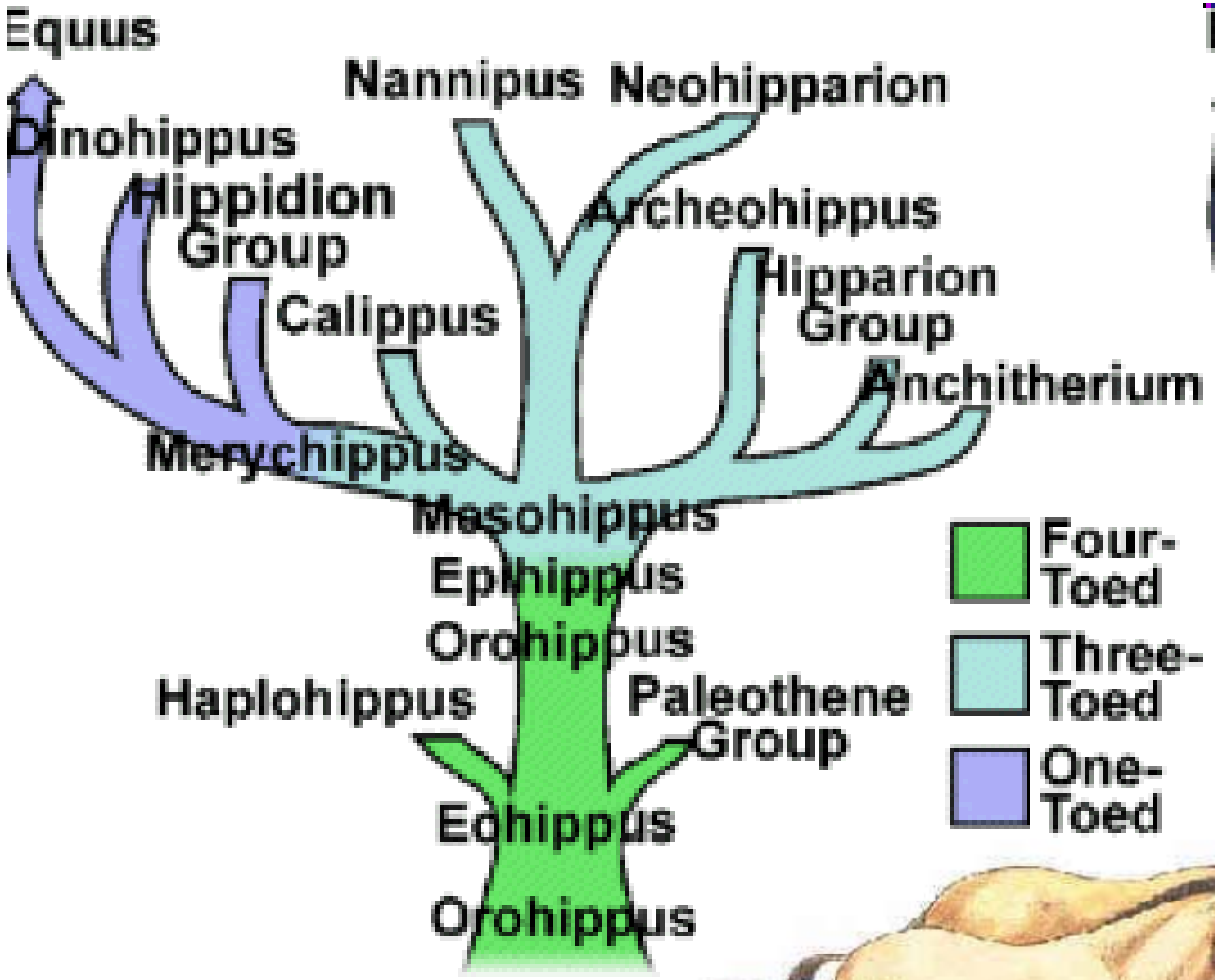
Adaptive Radiation

(a) Species of *Anolis* vary in leg length and tail length. Some species are ground dwelling; others live in distinct regions of shrubs or trees.

(b) The same adaptive radiation of *Anolis* has occurred on different islands, starting from different types of colonists.

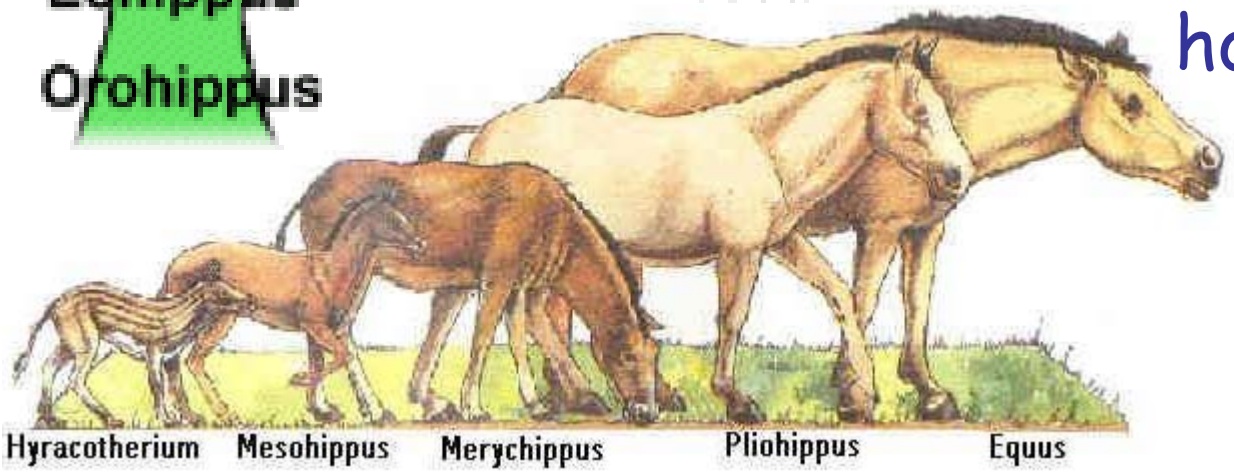


Expand and diversify into areas without competition (Area either 1) new or 2) former residents extinct.)



Most are EXTINCT!

Modern horse



http://www.critters-2-go.com/prehistoric/horse-evolution-species.jpg

Hox Gene Duplication

Living fossils: Gingko

(a) Triassic

(b)

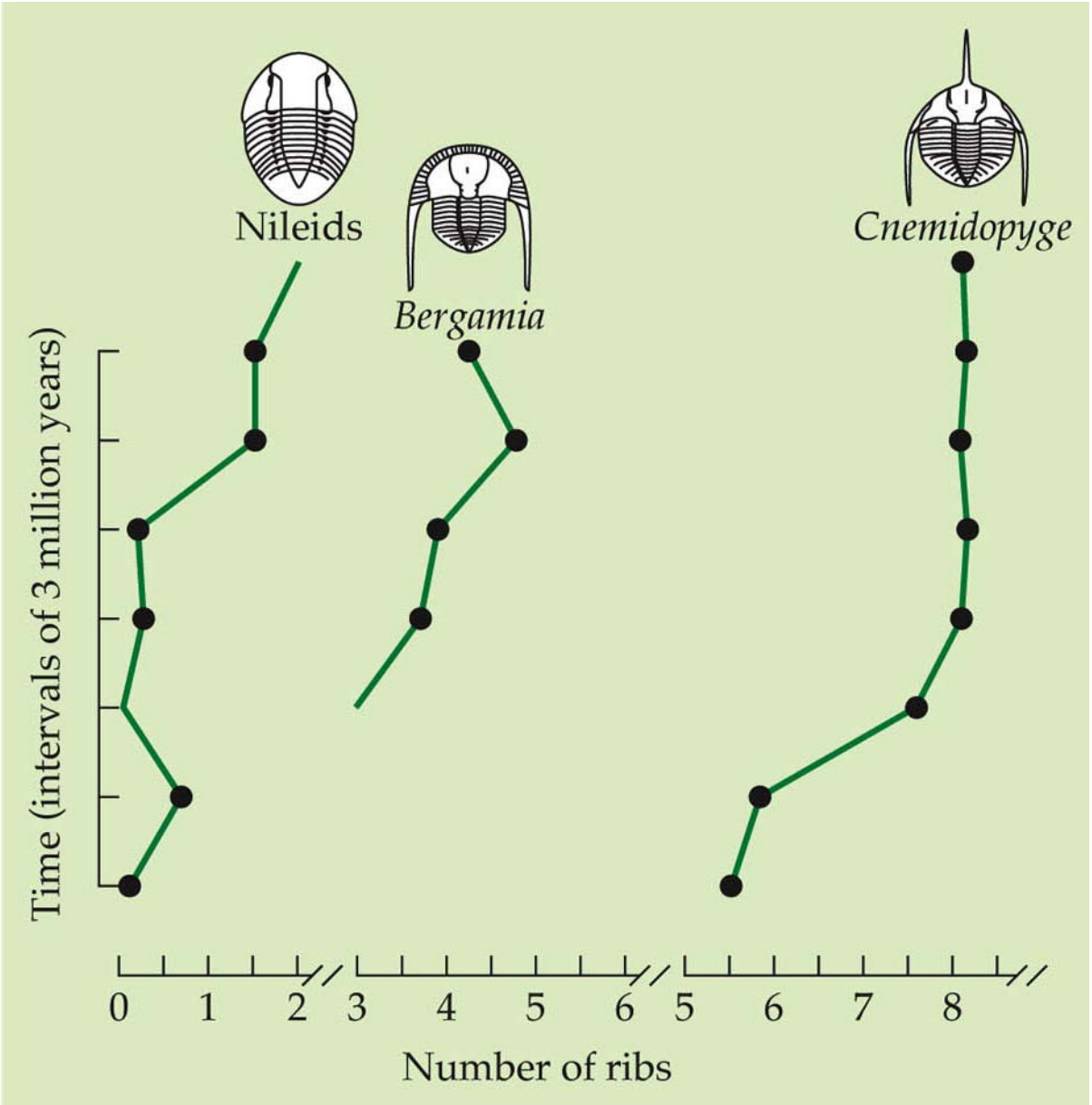
Living fossils: Horseshoe crabs

(b) *Limulus polyphemus*

~identical for 300 mya

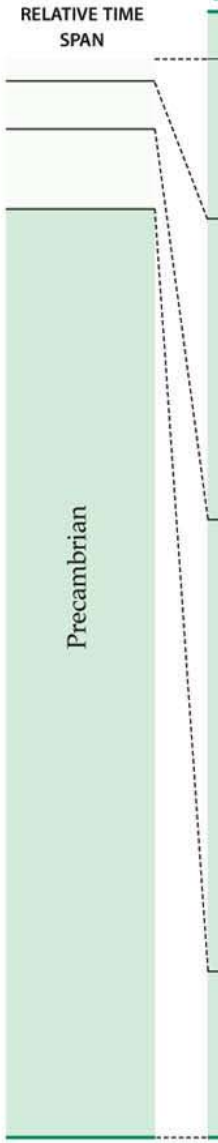
sandy coastlines are harsh environments that changed little, so they didn't need to evolve anything different

Gradual change: trilobite rib number



fossils show number of ribs

Biological history

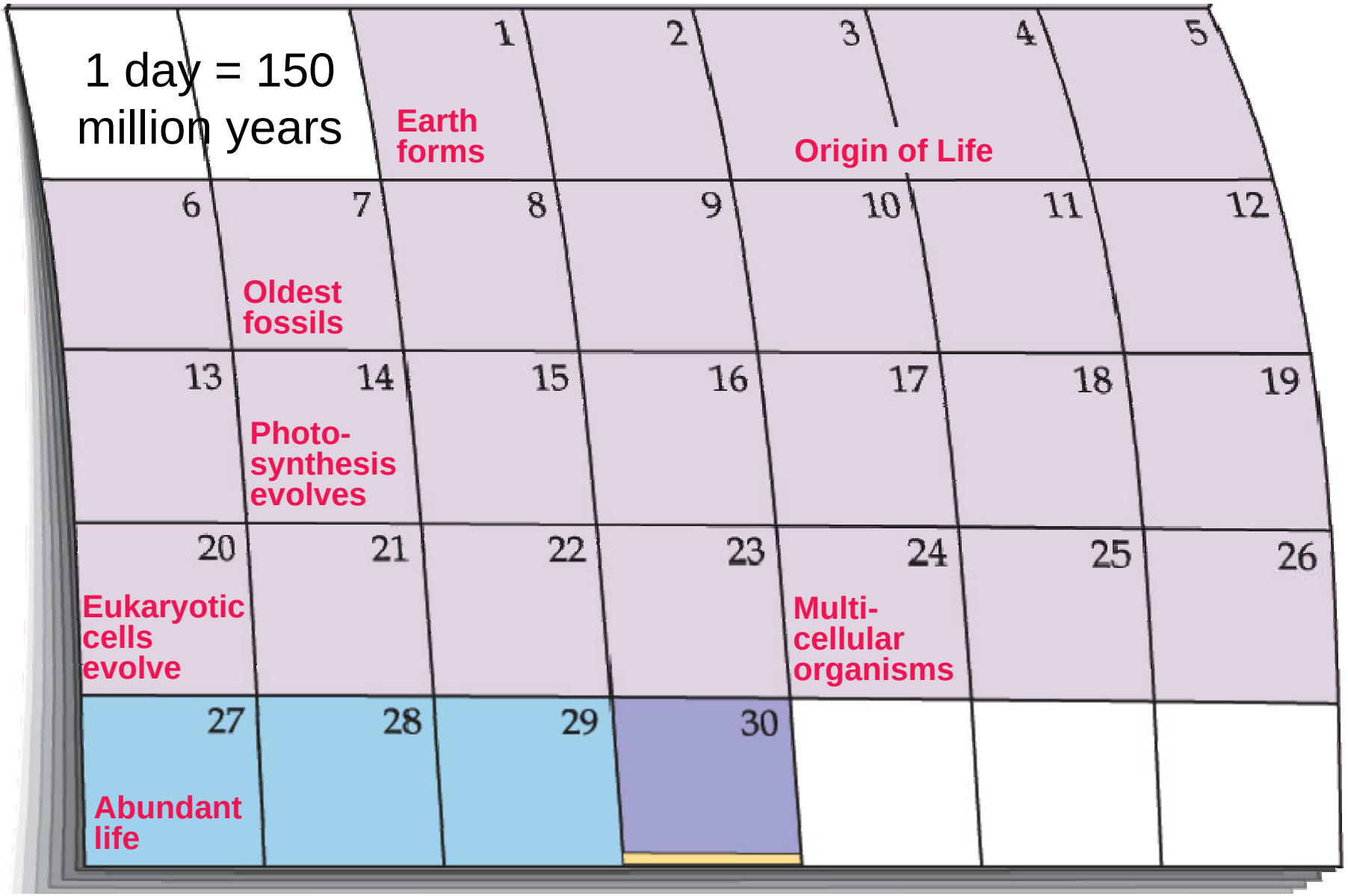


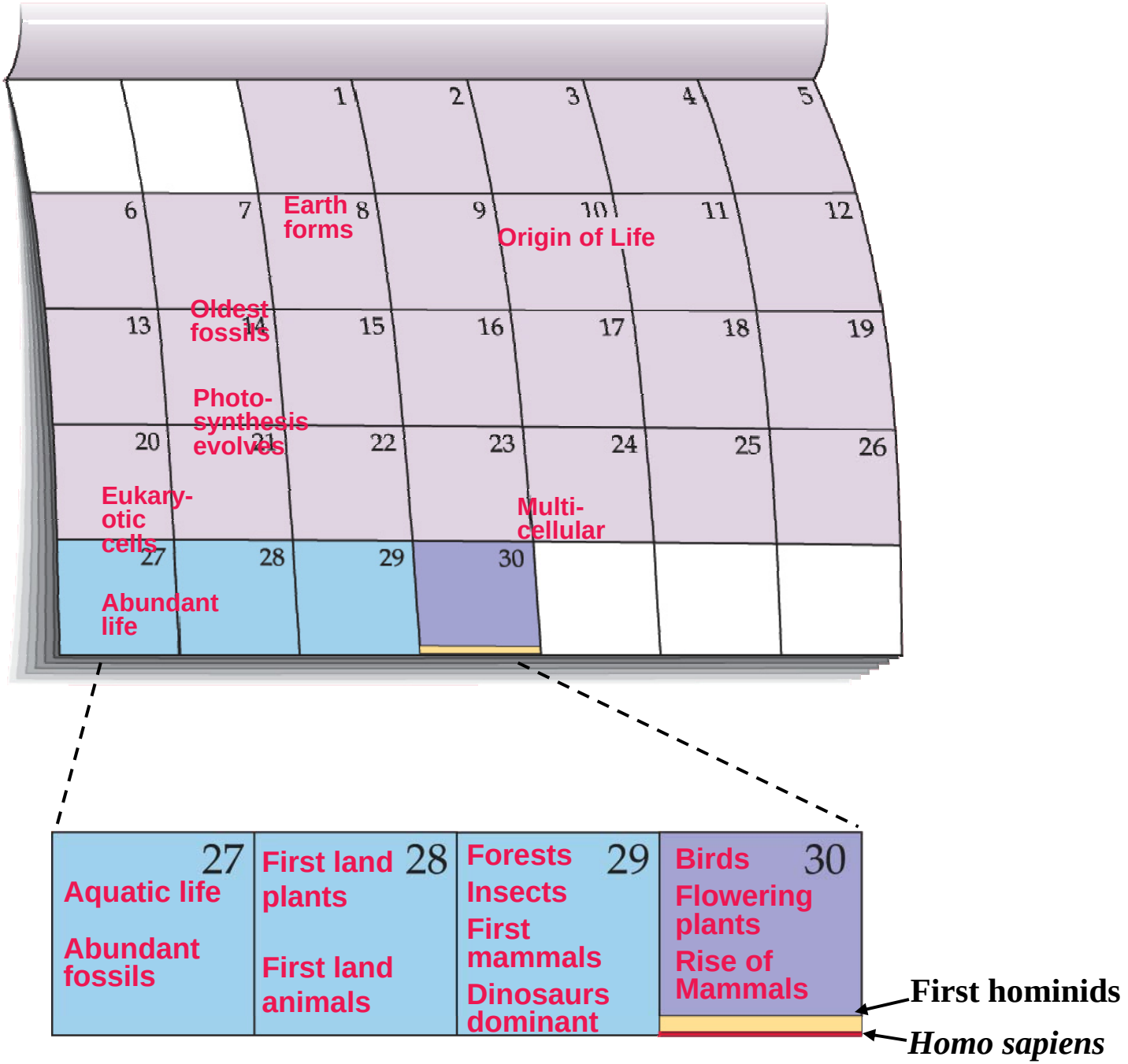
22.1 *Earth's Geological History* (Part 2)

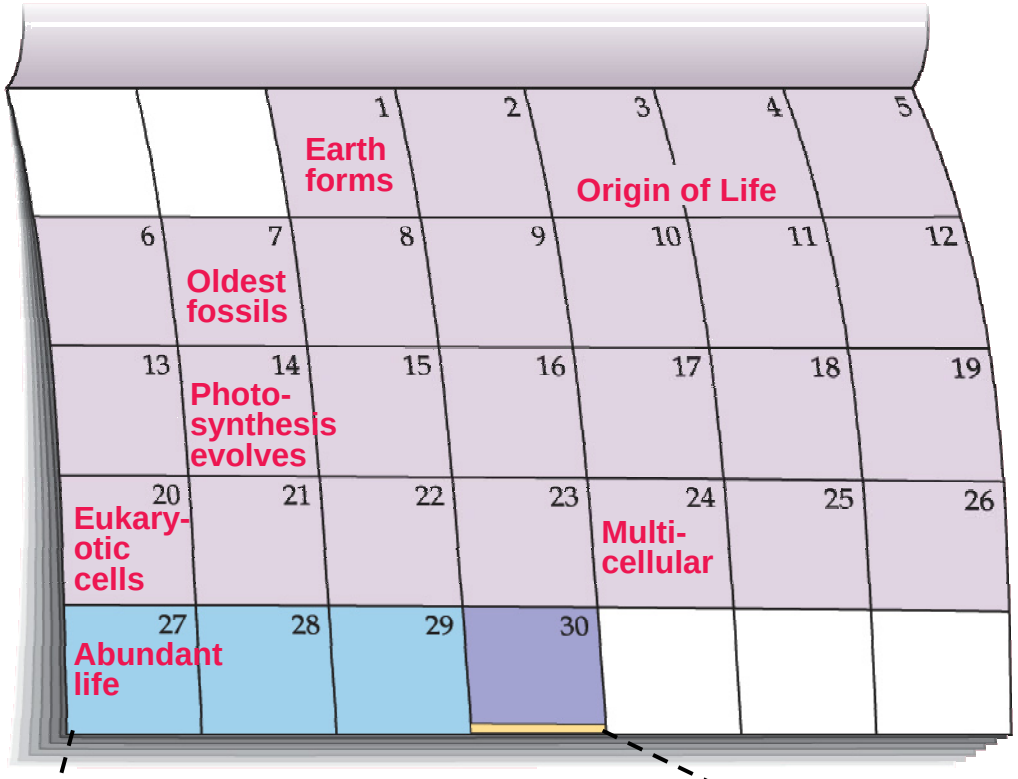
ERA	PERIOD	ONSET	MAJOR EVENTS IN THE HISTORY OF LIFE
Cenozoic	Quaternary	1.8 mya[a]	Humans evolve; many large mammals become extinct
	Tertiary	65 mya	Diversification of birds, mammals, flowering plants, and insects
Mesozoic	Cretaceous	144 mya	Dinosaurs continue to diversify; flowering plants and mammals diversify. **Mass Extinction** at end of period (≈76% of species disappear)
	Jurassic	206 mya	Diverse dinosaurs; radiation of ray-finned fishes
	Triassic	248 mya	Early dinosaurs; first mammals; marine invertebrates diversify; first flowering plants; **Mass Extinction** at end of period (≈65% of species disappear)
Paleozoic	Permian	290 mya	Reptiles diversify; amphibians decline; **Mass Extinction** at end of period (≈96% of species disappear)
	Carboniferous	354 mya	Extensive "fern" forests; first reptiles; insects diversify
	Devonian	417 mya	Fishes diversify; first insects and amphibians. **Mass Extinction** at end of period (≈75% of species disappear)
	Silurian	443 mya	Jawless fishes diversify; first ray-finned fishes; plants and animals colonize land
	Ordovician	490 mya	**Mass Extinction** at end of period (≈75% of species disappear)
	Cambrian	543 mya	Most animal phyla present; diverse algae
Precambrian		600 mya	Ediacaran fauna
		1.5 bya[a]	Eukaryotes evolve; several animal phyla appear
		3.8 bya	Origin of life; prokaryotes flourish
		4.5 bya	

[a]mya, million years ago; bya, billion years ago.

Biological history

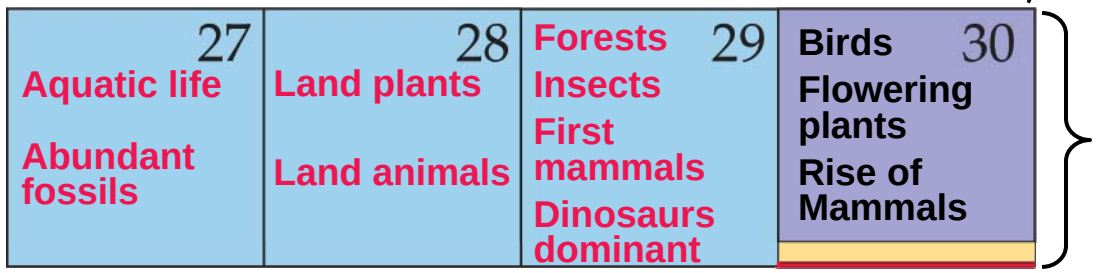


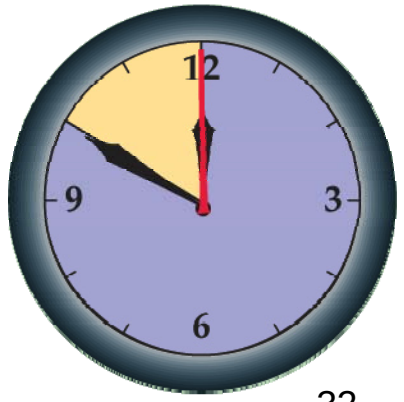

1
2
3
4
5
6
7
Earth forms
8
9
10
Origin of Life
11
12
13
14
Oldest fossils
15
16
17
18
19
20
21
Photo-synthesis evolves
22
23
24
25
26
Eukary-otic cells
Multi-cellular
27
28
29
30
Abundant life
27
Aquatic life
Abundant fossils
First land plants 28
First land animals
Forests 29
Insects
First mammals
Dinosaurs dominant
Birds 30
Flowering plants
Rise of Mammals
First hominids
Homo sapiens

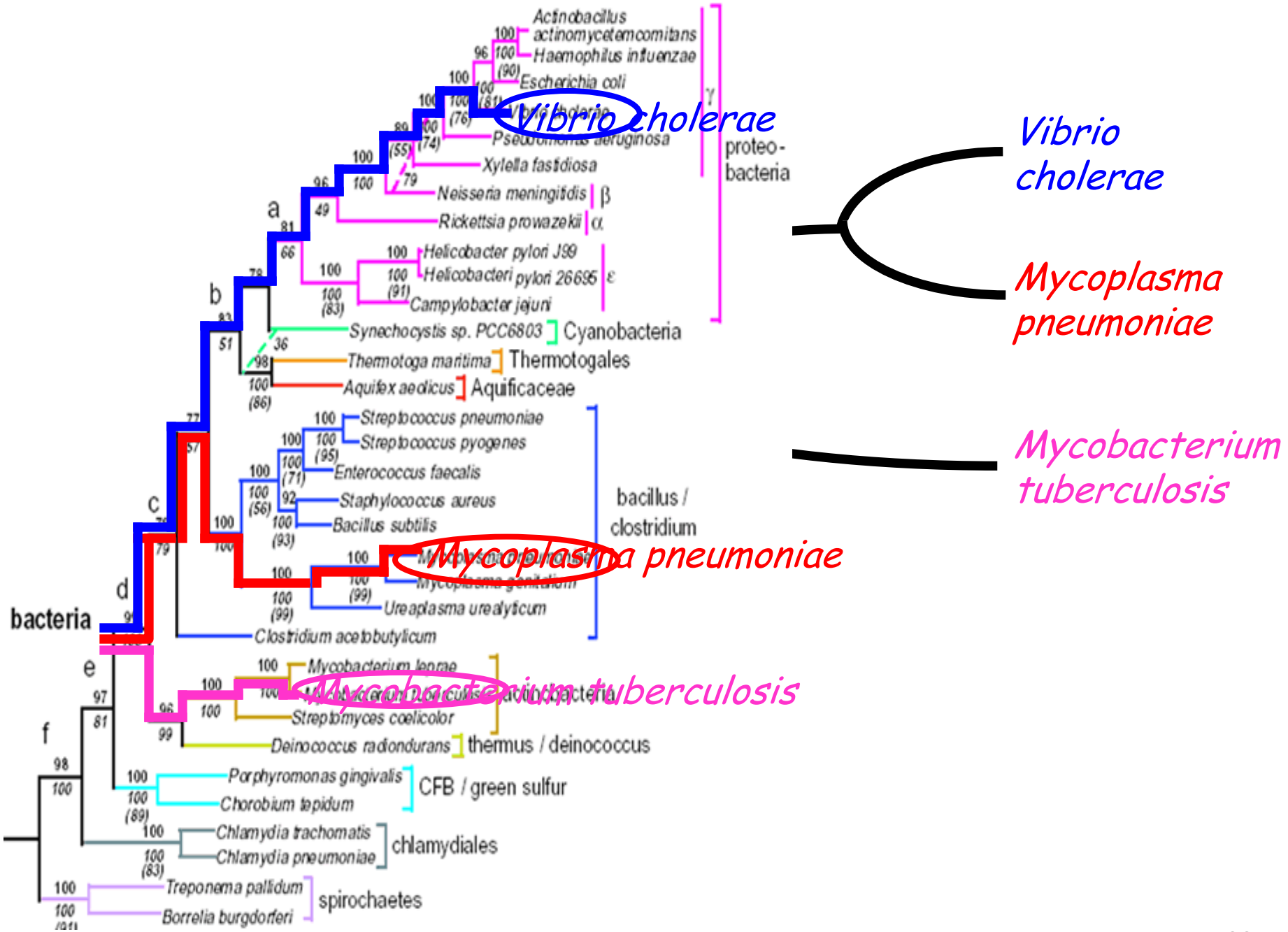


Recorded history fills the last 5 seconds of day 30.

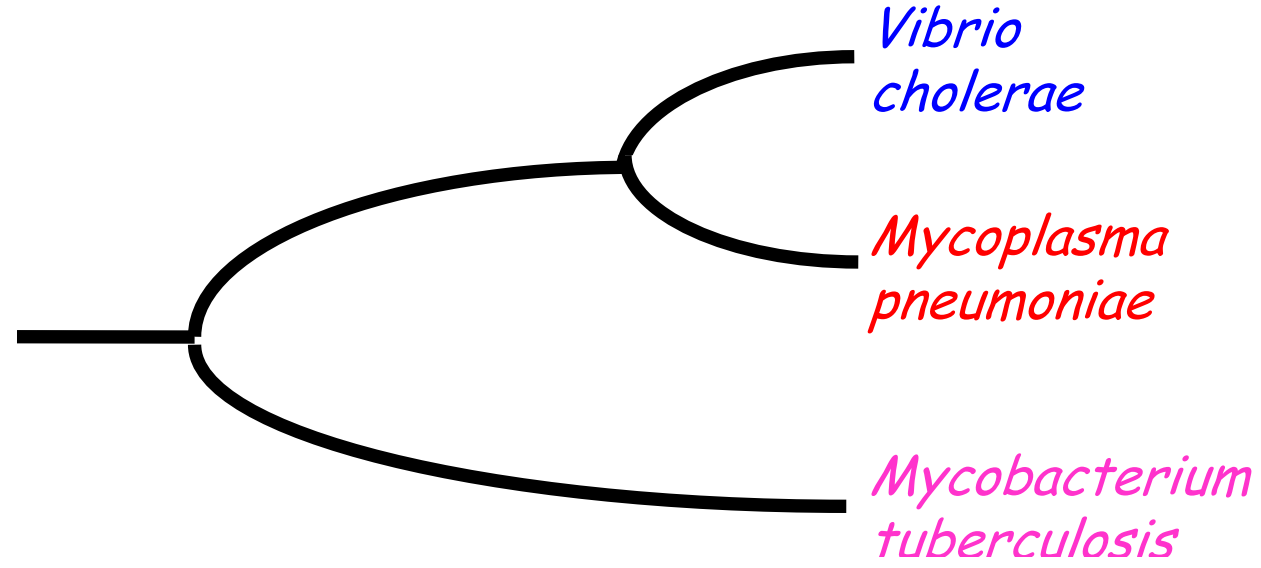
Modern humans appeared in the last 10 minutes of day 30.

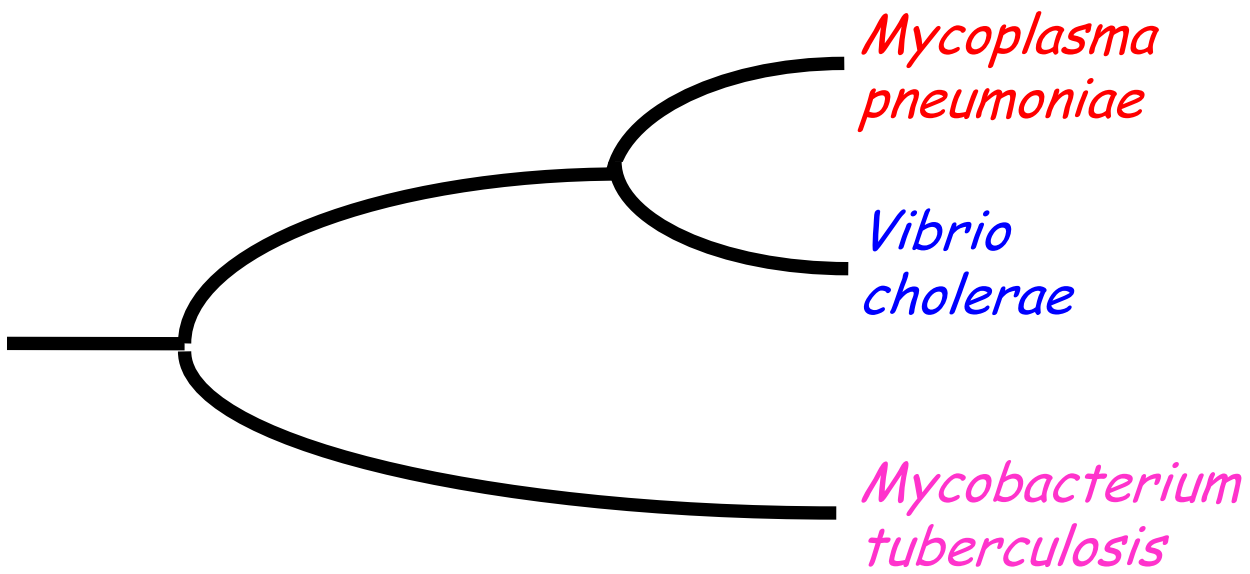





Actinobacillus actinomycetemcomitans
Haemophilus influenzae
Escherichia coli
Vibrio cholerae
Pseudomonas aeruginosa
Xylella fastidiosa
Neisseria meningitidis
Rickettsia prowazekii
Helicobacter pylori J99
Helicobacter pylori 26695
Campylobacter jejuni
Synechocystis sp. PCC6803
Thermotoga maritima
Aquifex aeolicus
Streptococcus pneumoniae
Streptococcus pyogenes
Enterococcus faecalis
Staphylococcus aureus
Bacillus subtilis
Mycoplasma pneumoniae
Mycoplasma genitalium
Ureaplasma urealyticum
Clostridium acetobutylicum
Mycobacterium leprae
Mycobacterium tuberculosis
Streptomyces coelicolor
Deinococcus radiodurans
Porphyromonas gingivalis
Chlorobium tepidum
Chlamydia trachomatis
Chlamydia pneumoniae
Treponema pallidum
Borrelia burgdorferi
proteo-bacteria
γ
β
α
ε
Cyanobacteria
Thermotogales
Aquificaceae
bacillus / clostridium
actinobacteria
thermus / deinococcus
CFB / green sulfur
chlamydiales
spirochaetes
bacteria
a
b
c
d
e
f
Vibrio cholerae
Mycoplasma pneumoniae
Mycobacterium tuberculosis
Vibrio cholerae
Mycoplasma pneumoniae
Mycobacterium tuberculosis

These trees are the same





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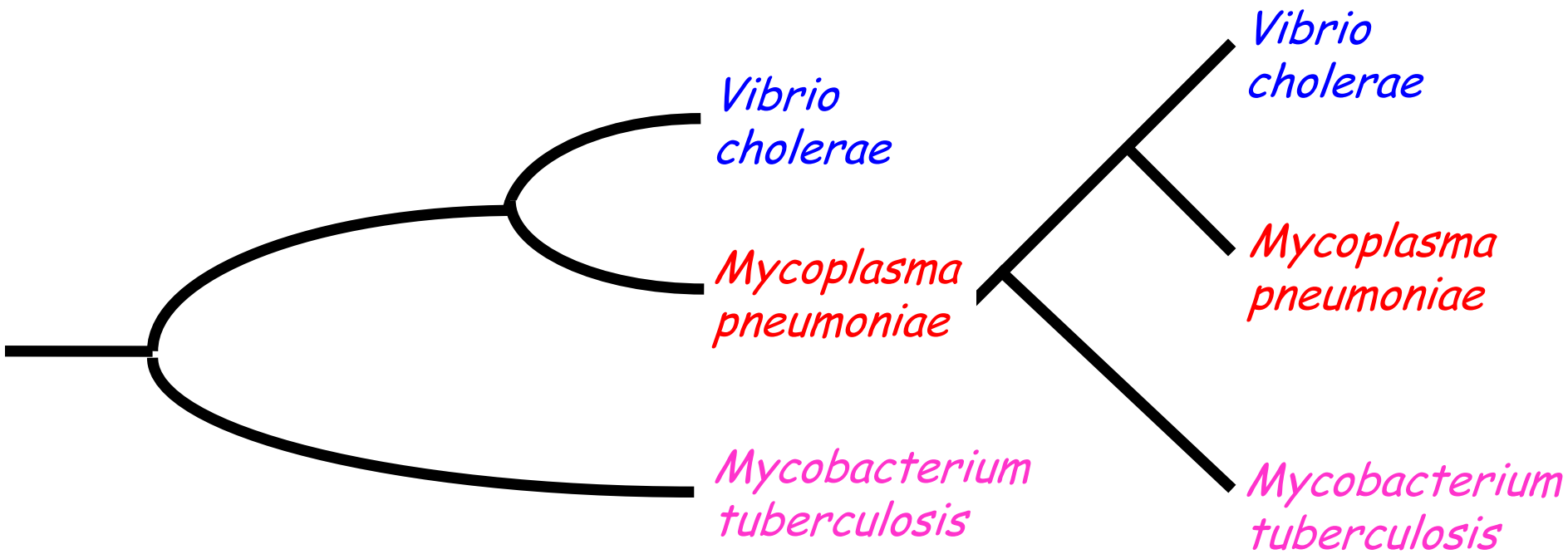
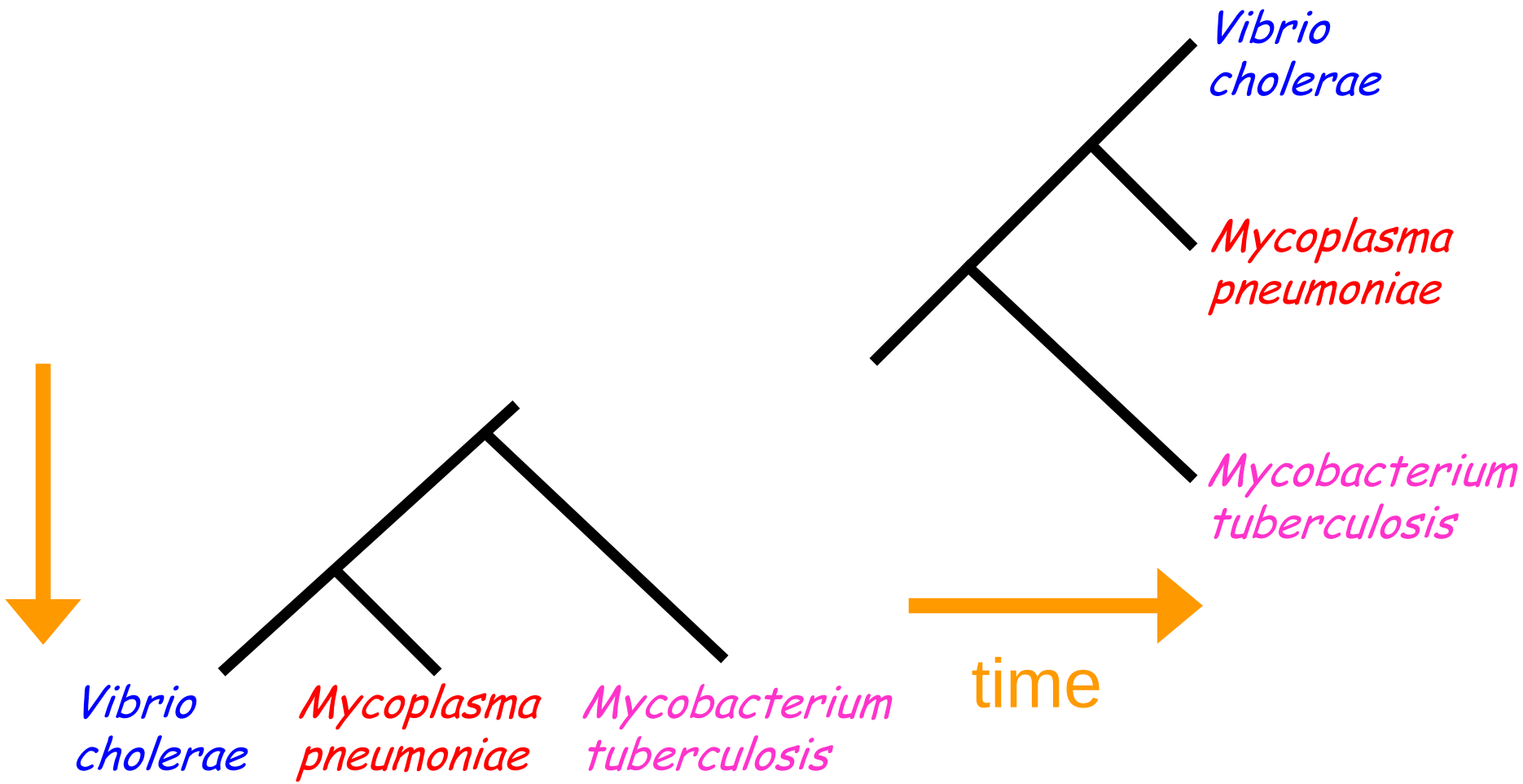
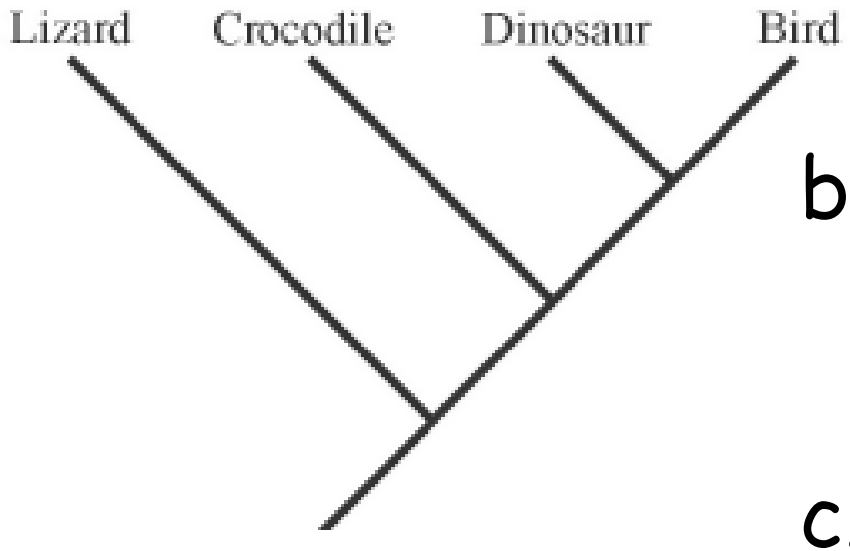


These trees are the same



Which of these statements follows from the tree?

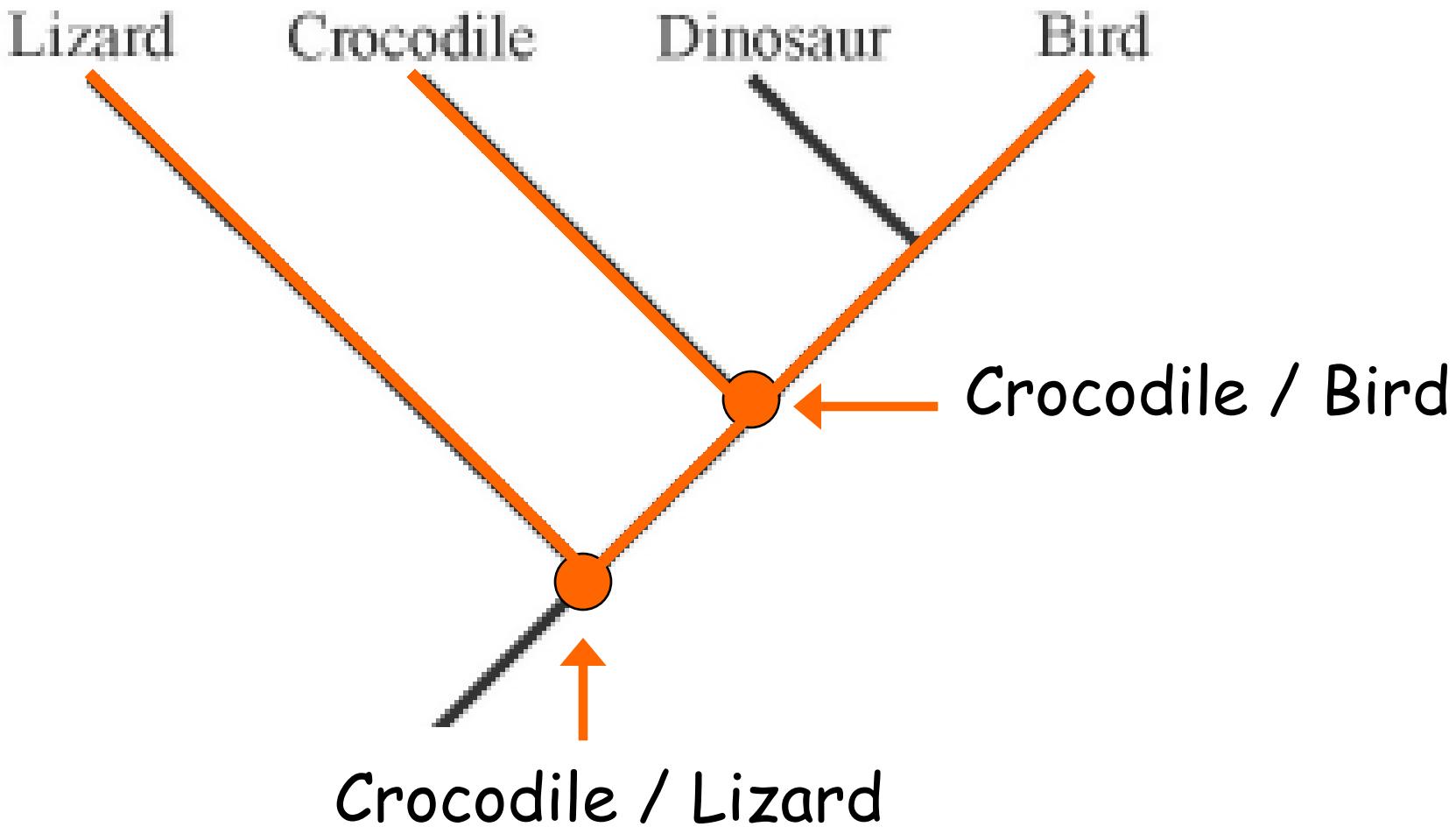


a. Crocodiles are more closely related to lizards than to birds

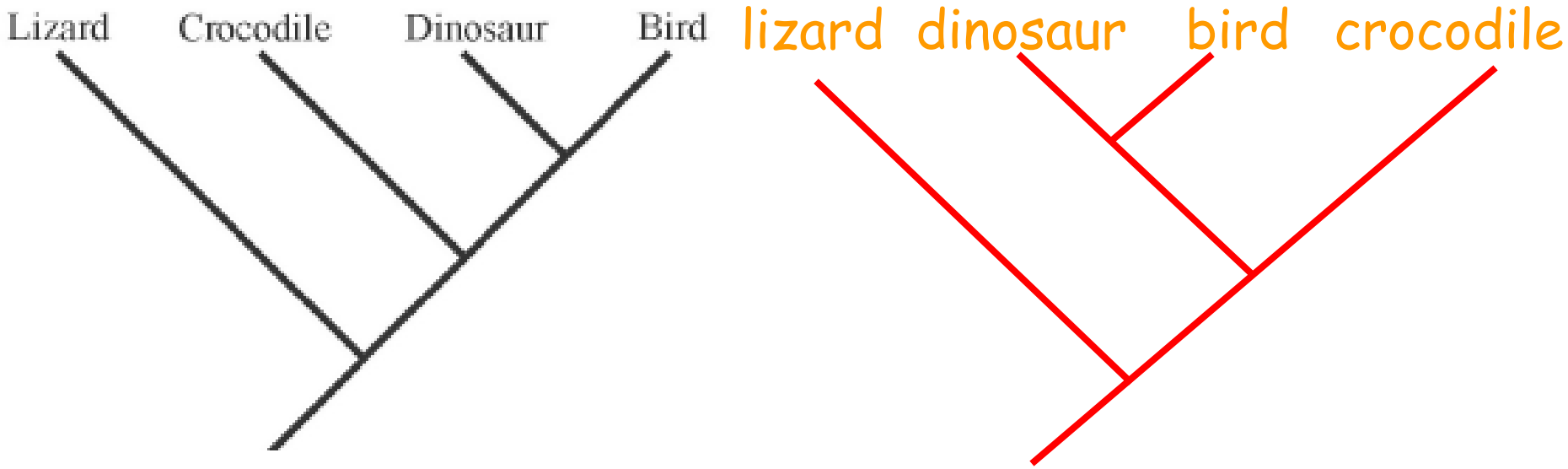
b. Crocodiles are more closely related to birds than to lizards

c. Crocodiles are equally related to lizards and birds

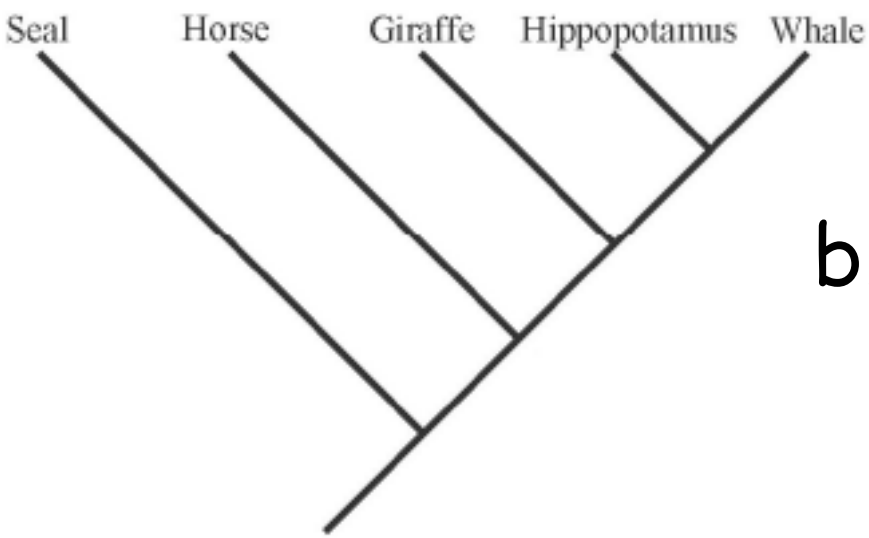
Focus on nodes = common ancestors



Another method: redraw tree with focus on crocodile



Which of these statements follows from the tree?



a. A seal is more closely related to a horse than to a whale.

b. A seal is more closely related to a whale than to a horse.

c. A seal is equally related to a whale and a horse.

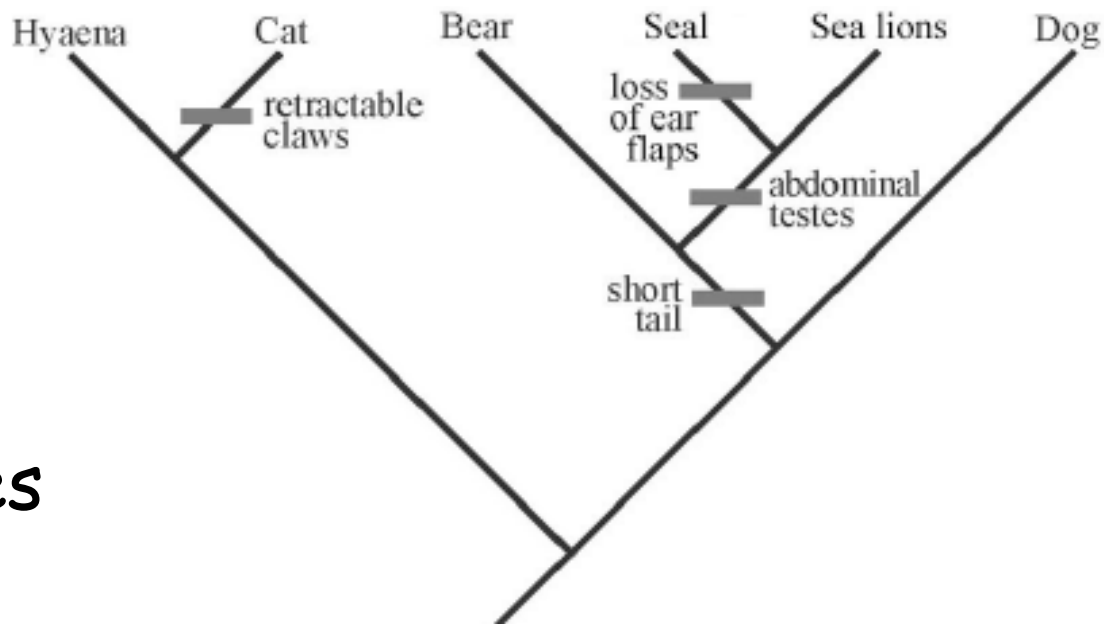
Ancestral traits

- Traits inherited from ancestor in distant past should be shared by large number of species
- Traits that first appeared in more recent ancestor should be shared by fewer species
- Ancestral trait = shared traits inherited from a common ancestor
- Derived trait = different from ancestral form

Nucleic acids are an ancestral trait

- Nucleic acids (DNA/RNA) as genetic material is ancestral to all life on Earth
- Specific genetic code is ancestral to most

The ancestor to this tree had a long tail, ear flaps, external testes, and fixed claws. Based on the tree, what traits does a sea lion have?



a. long tail, ear flaps, external testes, and fixed claws
b. short tail, no ear flaps, external testes, and fixed claws
c. short tail, no ear flaps, abdominal testes, and fixed claws
d. short tail, ear flaps, abdominal testes, and fixed claws
e. long tail, ear flaps, abdominal testes, and retractable claws

Ancestral vs derived may depend on scale of taxa

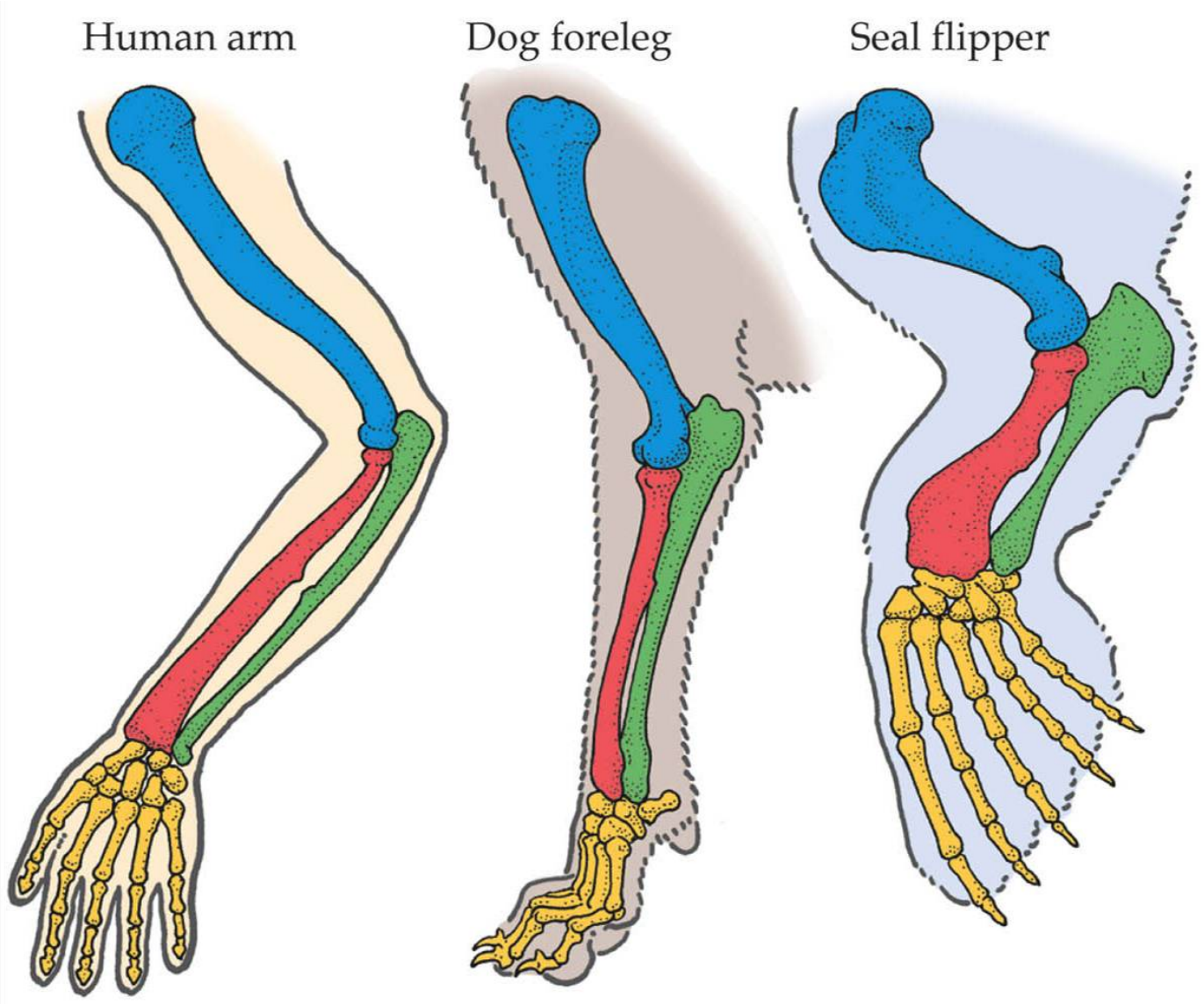
- In rodents: continuously growing incisors are ancestral: all rodents have them
- In mammals they are derived, unique to rodents

Homologous traits

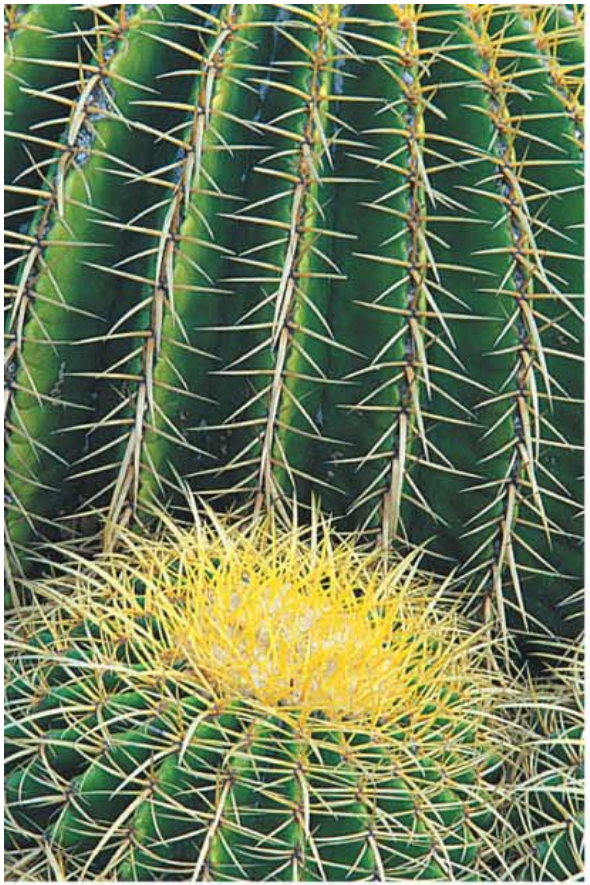
- Features (DNA sequence, behavior, morphology) shared by species descended from common ancestor are called **homologous**

- e.g., vertebral column is homologous in vertebrates

Mammalian limbs are homologous, even with different functions



Homologous structures derived from leaves

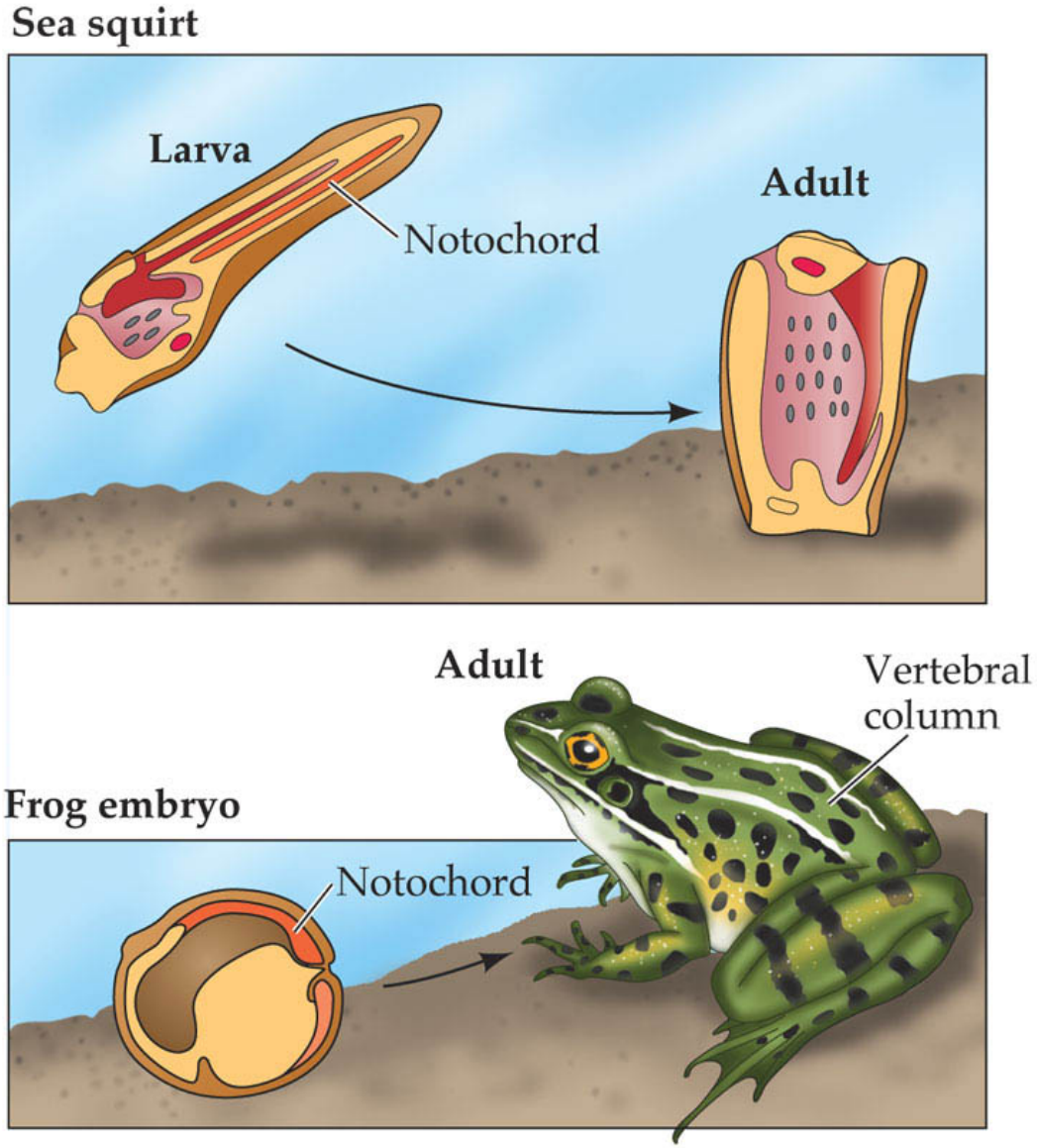


Cheiridopsis tuberculata

Heliconia sp.

Sarracenia purpurea

Some homologies are hidden by development



Notochord homology seen only in early development, invisible in adult

Both in Phylum Chordata

Deducing phylogeny

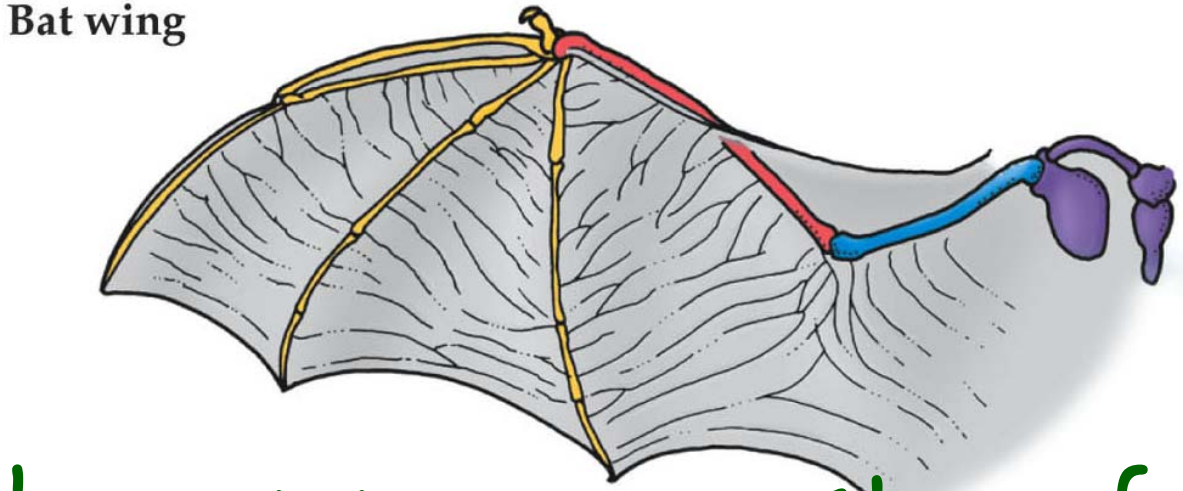
Look at shared traits

- What is ancestral state?
- How has it been modified?

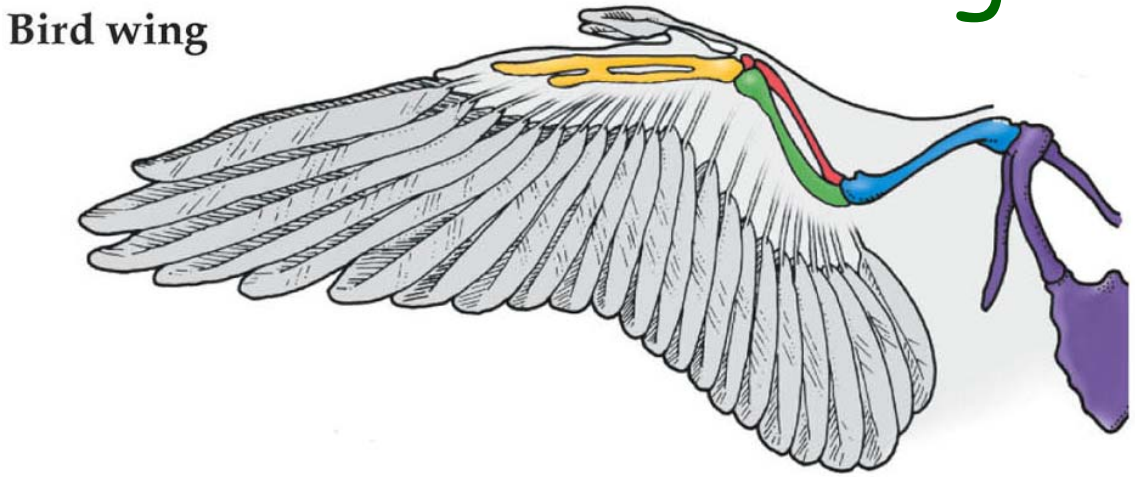
Two processes make this difficult

- 1. Convergent evolution = similar selective pressures make independently evolved traits look superficially similar
- 2. Evolutionary reversal = character reverts from derived state back to ancestral state

Bird and bat bones are homologous, but not wings (convergent evolution)



Did the common ancestor of birds and bats have wings?

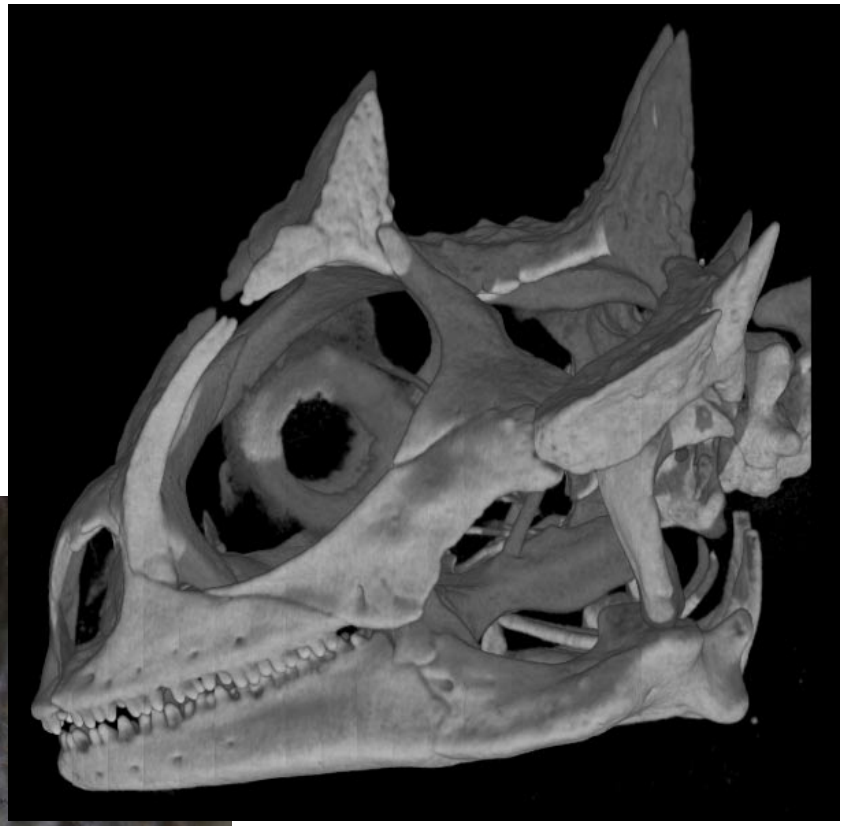


Homoplastic traits

Convergent evolution and evolutionary reversal generate homoplasies: traits that are similar for some reason other than inheritance from a common ancestor

Bird and bat wings are homoplastic

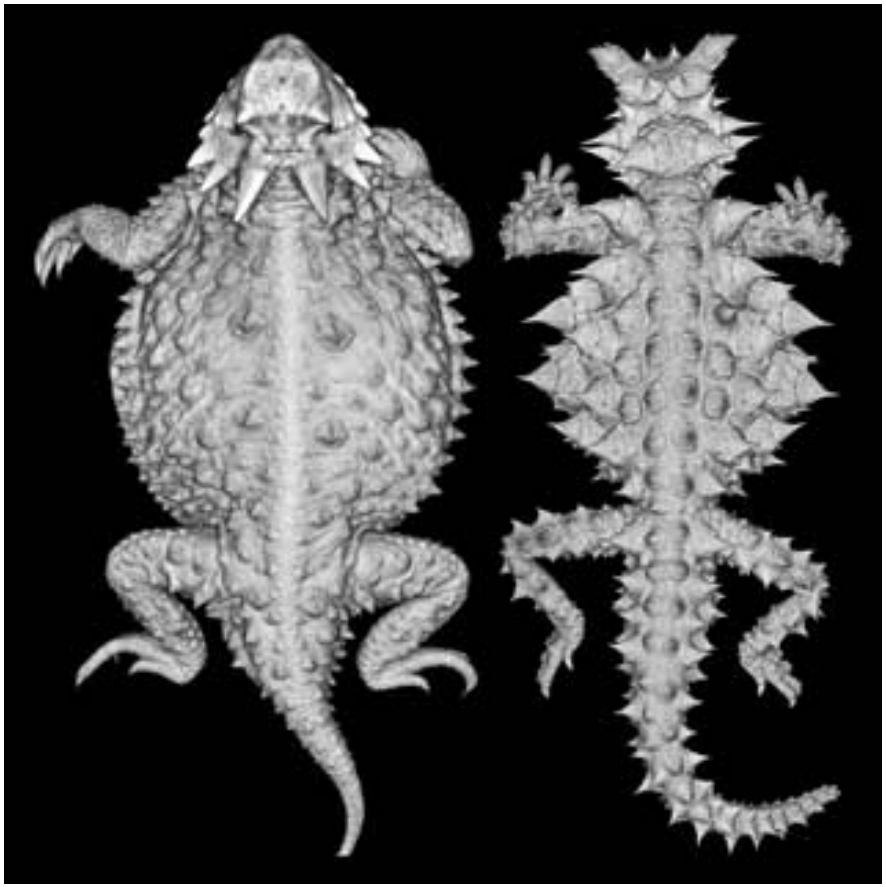
Phrynosoma asio,
Long-spined
Horned Lizard
MEXICO



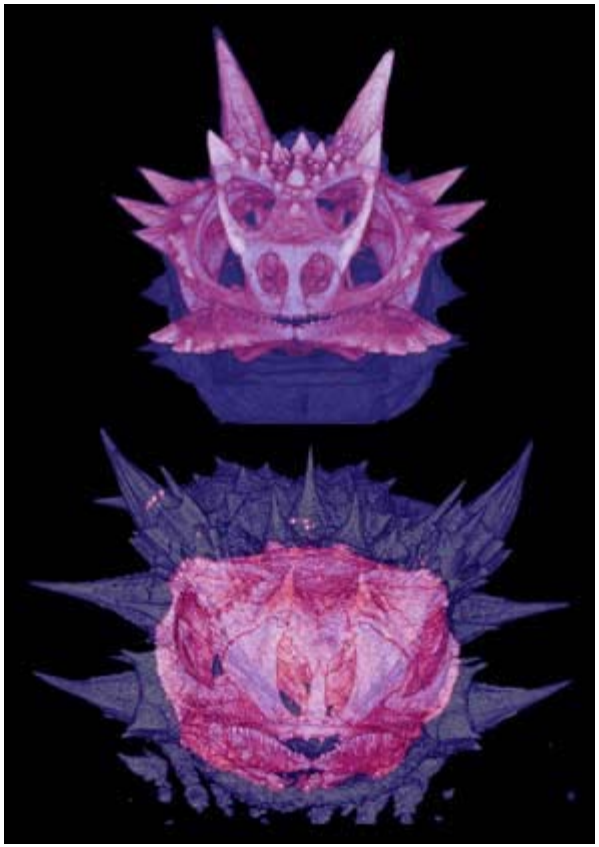
http://digimorph.org/specimens/Phrynosoma_asio/

Moloch horridus, Thorny Devil, AUSTRALIA

Spiny head: Homoplasy or Homology?



Phrynosoma cornutum (left) vs. *Moloch horridus* (right)



P. cornutum (top) vs. *M. horridus* (bottom); semi-transparent flesh in blue, bone in red

All of the following can result in homoplasy except

a. similar selection pressures.

b. reverse evolution.

c. parallel evolution.

d. descent from a recent common ancestor.

e. convergent evolution.

Creating a phylogeny

1. Choose the characters and identify the possible forms (traits) of the characters
2. Determine ancestral and derived traits
3. Distinguish homologous from homoplastic traits

Traditional character choice

- Most often morphology
  - describes size and shape of body parts
  - can be seen directly in fossil record
- Also physiological, behavioral, molecular and structural traits as available
- The more characters measured, the more the inferred phylogenies should converge on each other and on the real evolutionary pattern

Simple phylogeny example

- Choose 8 vertebrate species and hypothesize their phylogeny
- Traits either present (+) or absent (-)
- Assume that each derived trait evolved only once and that no derived traits were lost

TAXON	JAWS	LUNGS	CLAWS OR NAILS	GIZZARD
Lamprey	–	–	–	–
Perch	+	–	–	–
Salamander	+	+	–	–
Lizard	+	+	+	–
Crocodile	+	+	+	+
Pigeon	+	+	+	+
Mouse	+	+	+	–
Chimpanzee	+	+	+	–

TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS SCALES
Lamprey	–	–	–	–
Perch	–	–	–	–
Salamander	–	–	–	–
Lizard	–	–	–	+
Crocodile	–	–	–	+
Pigeon	+	–	–	+
Mouse	–	+	+	–
Chimpanzee	–	+	+	–

Determine ancestral and derived traits

- Chimp and mouse share mammary glands and fur, other animals lack them
- Ancestral or derived? derived

TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS SCALES
Lamprey	–	–	–	–
Perch	–	–	–	–
Salamander	–	–	–	–
Lizard	–	–	–	+
Crocodile	–	–	–	+
Pigeon	+	–	–	+
Mouse	–	+	+	–
Chimpanzee	–	+	+	–

Determine ancestral and derived traits

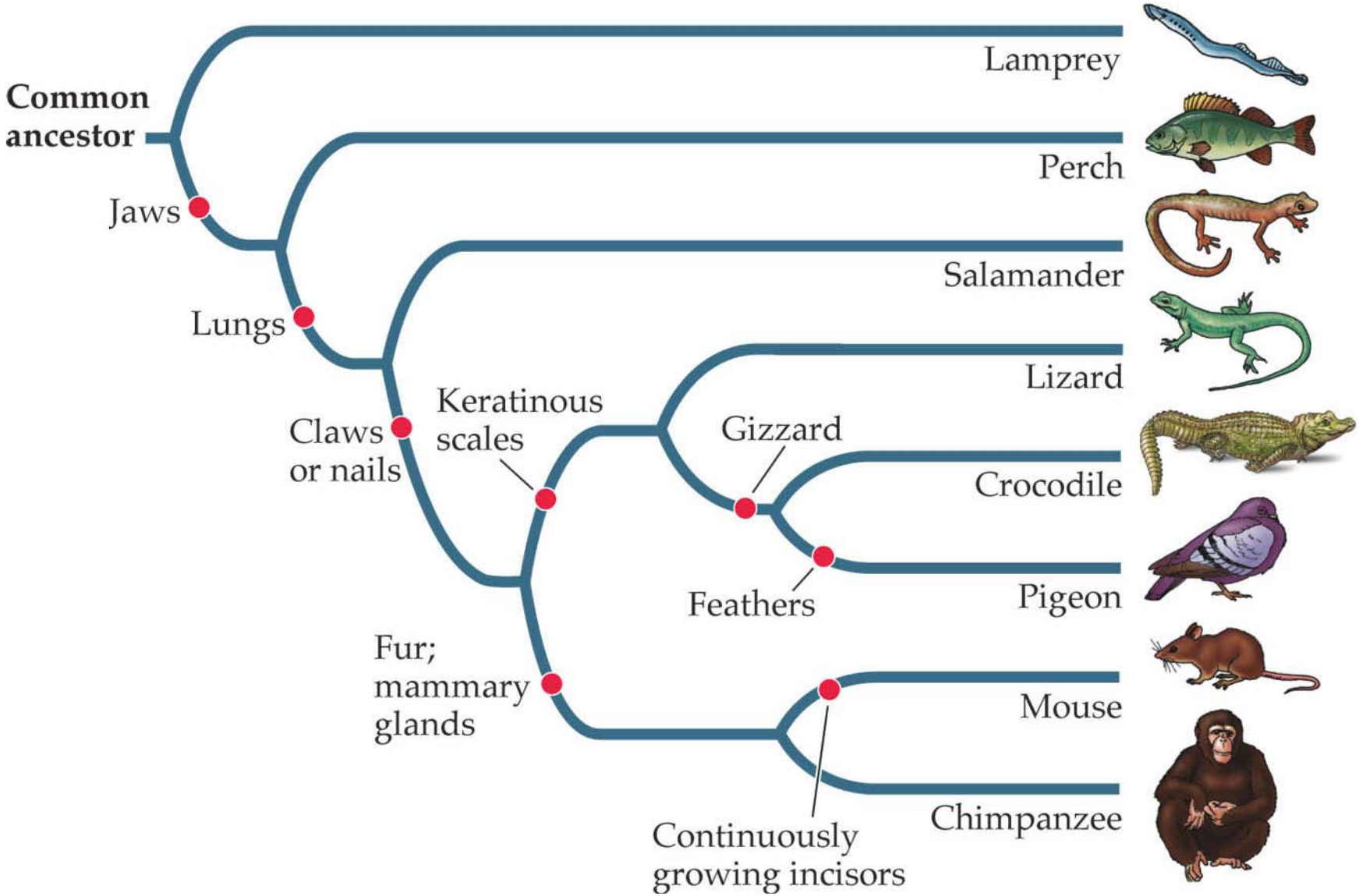
- Use similar reasoning on other traits
- Lamprey has no derived traits, so it is an outgroup

Your Turn…

TAXON	DERIVED TRAIT[a] JAWS	LUNGS	CLAWS OR NAILS	GIZZARD
Lamprey	–	–	–	–
Perch	+	–	–	–
Salamander	+	+	–	–
Lizard	+	+	+	–
Crocodile	+	+	+	+
Pigeon	+	+	+	+
Mouse	+	+	+	–
Chimpanzee	+	+	+	–

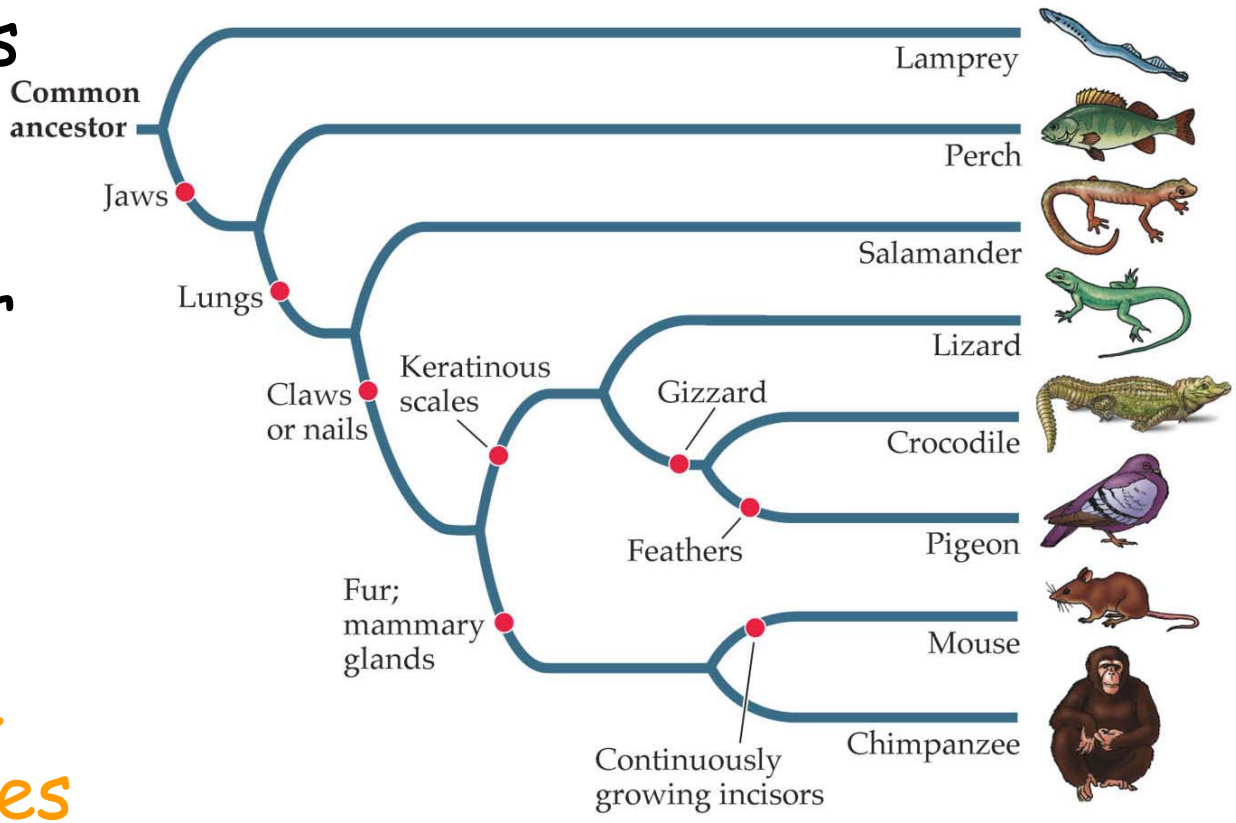
TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS SCALES
Lamprey	–	–	–	–
Perch	–	–	–	–
Salamander	–	–	–	–
Lizard	–	–	–	+
Crocodile	–	–	–	+
Pigeon	+	–	–	+
Mouse	–	+	+	–
Chimpanzee	–	+	+	–

Simple phylogeny example

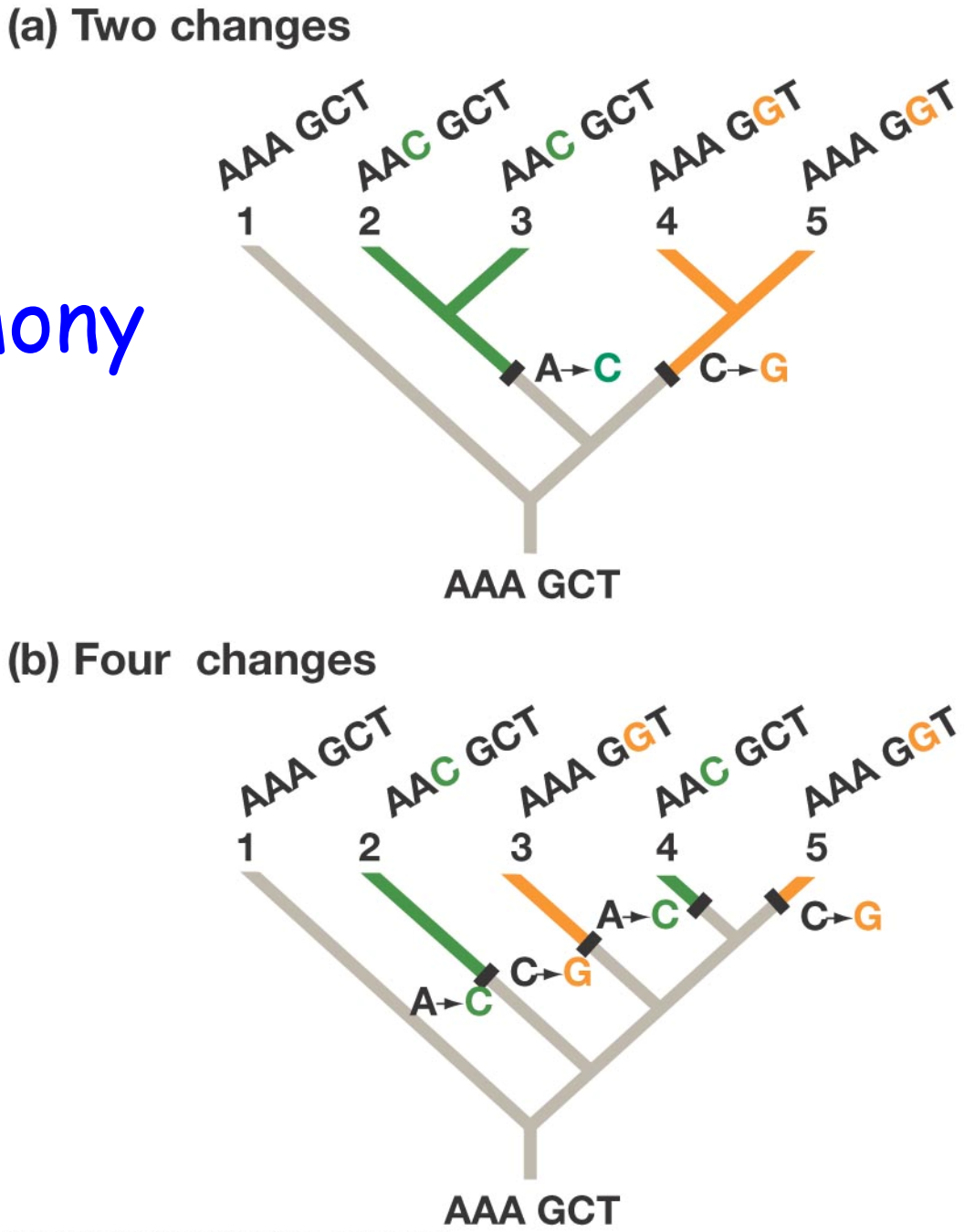


Not always so simple

- Assumed derived traits appeared once and were never lost
- If we had included snakes, this wouldn't have worked: they have scales but no claws
- Snakes lost limbs and claws during descent from a common ancestor with lizards
- Parsimony means we assume the smallest possible number of changes



Parsimony



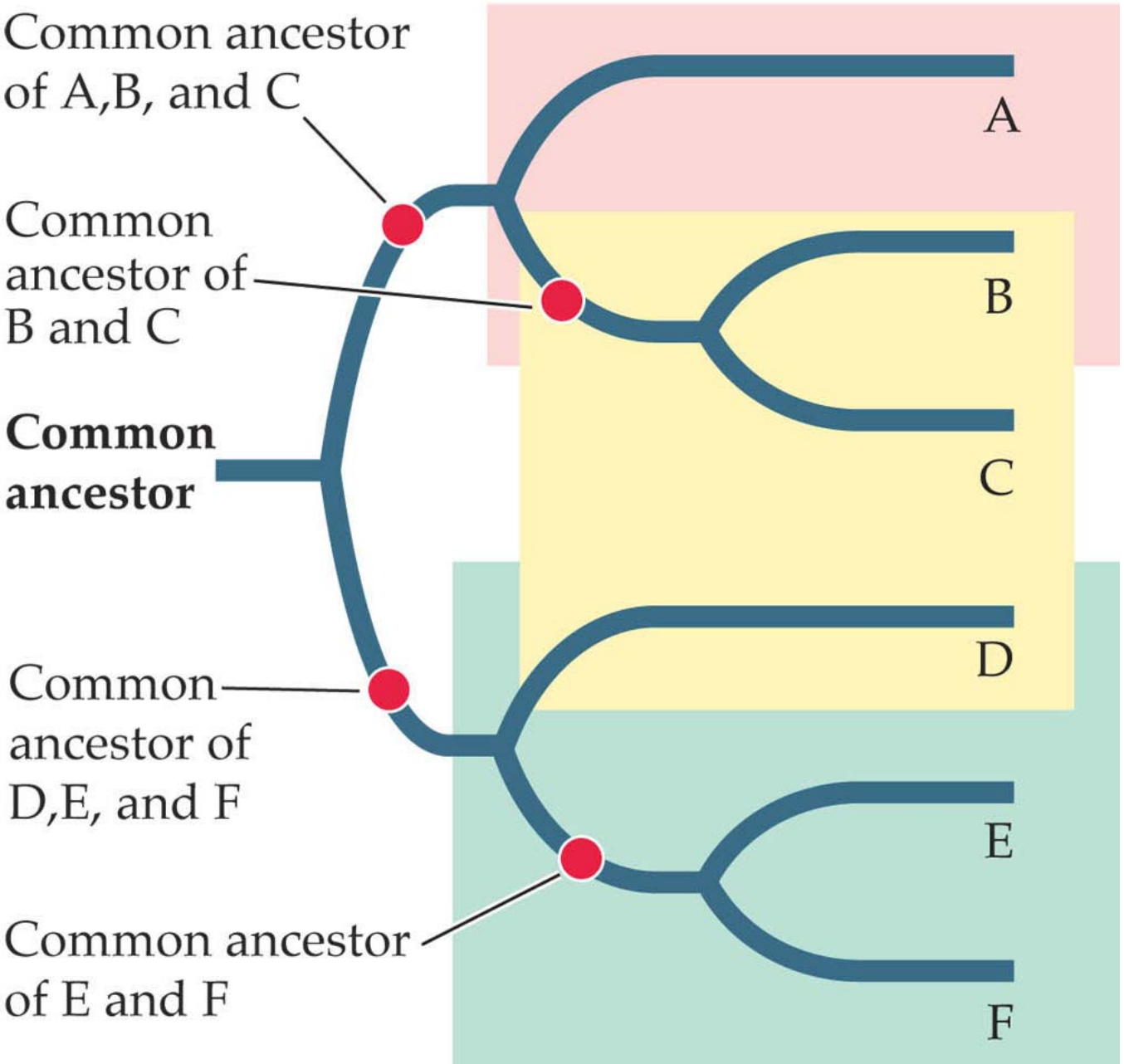
Modern character choice

Today, most phylogenies come from gene sequences

- DNA/RNA/protein

Classification should reflect evolutionary relationships

- A monophyletic group (or clade) contains all descendents of a particular ancestor and no other organisms (best)
- A polyphyletic taxon contains members with more than one recent common ancestor
- A paraphyletic group contains some, but not all of the descendents of a particular ancestor

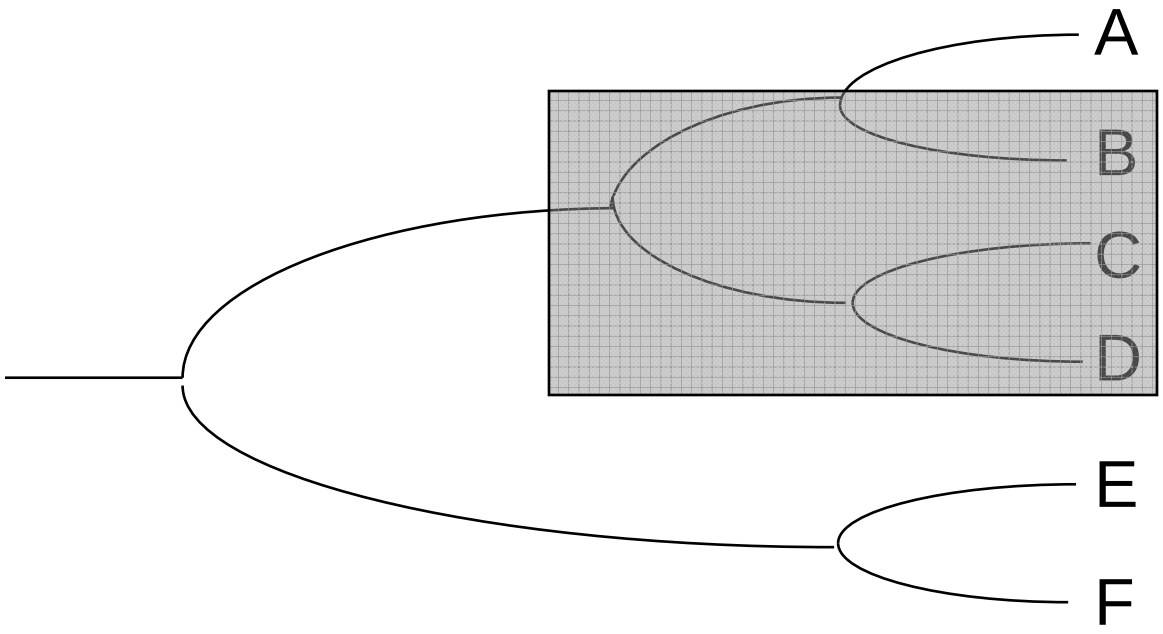


paraphyletic

polyphyletic

monophyletic

A group consisting of the shaded species is best described as

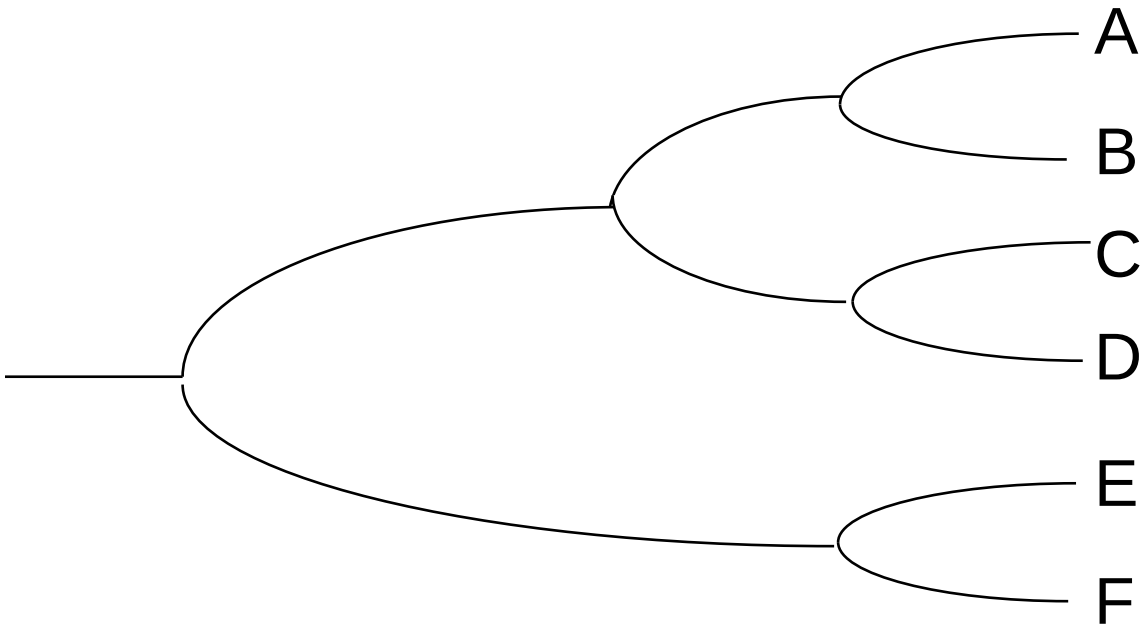


a. polyphyletic.

b. paraphyletic.

c. monophyletic.

A particular trait is found only in species A and E. Assuming that the phylogenetic tree is correct, the simplest model describes this trait as



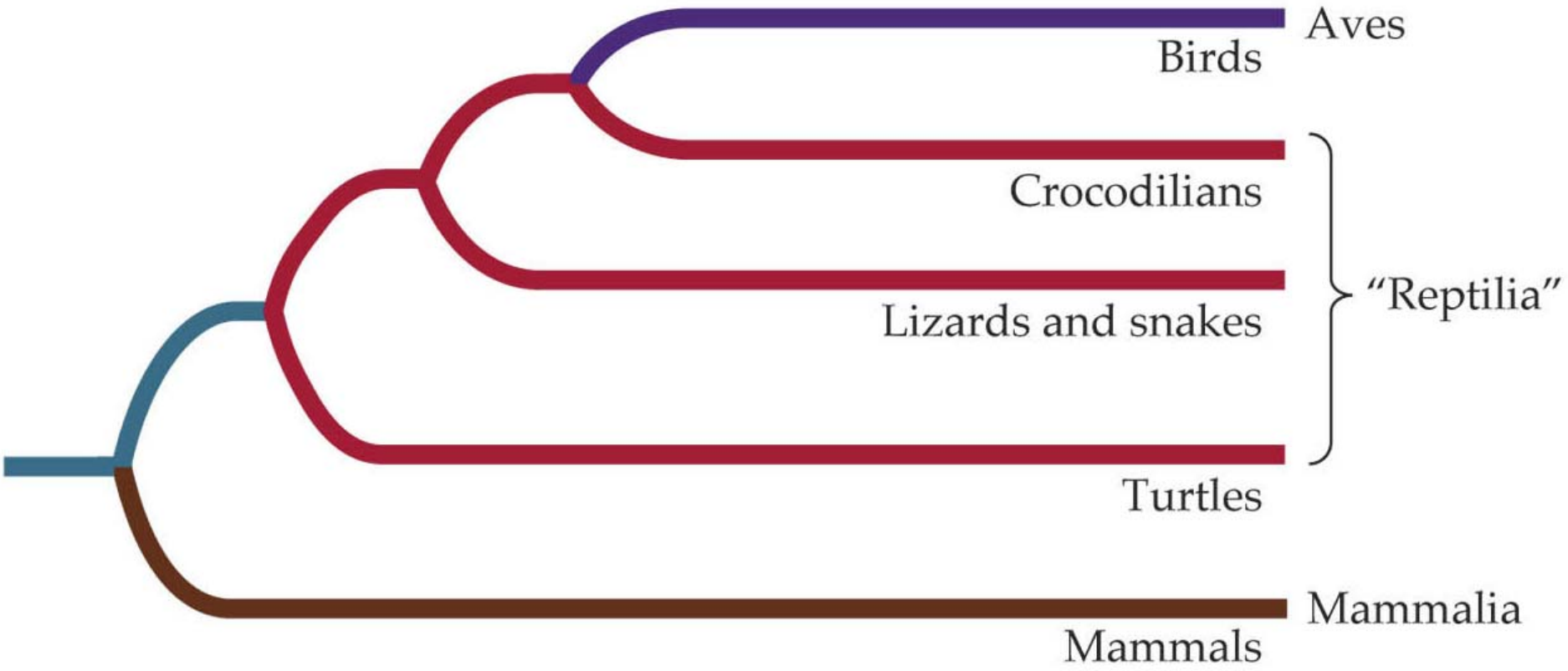
a. orthologous.

b. ancestral.

c. homoplastic.

d. homologous.

Should reptiles be a group?



Molecular evidence shows birds and crocodilians closer than crocodilians and other reptiles

Reptiles are paraphyletic, since birds excluded

Birds look very different

- Birds have rapidly evolved unique derived traits since they separated from reptiles
- Groups called grades have changed rapidly. May be an appropriate group even if paraphyletic
- General tendency to eliminate paraphyletic groups as we learn more, but some familiar categories, such as reptiles, won't disappear in a hurry

Uses of phylogenetic trees

1. How are different species related?
2. What traits do you expect a newly discovered species to have?
3. How many times has a trait evolved?
4. Which molecular change is responsible for adaptation?
5. When did lineages split?
   use DNA sequence and the "molecular clock"

The Evolution of Macromolecules

- The **neutral theory of molecular evolution**:
  - postulates that, at the molecular level, the majority of mutations are selectively neutral.
- Thus, macromolecule evolution, and much of the genetic variation within species, does not result from positive selection of advantageous alleles nor stabilizing selection.
- Mutation fixation rate is theoretically constant and equal to the neutral mutation rate – a molecular clock.
  - The concept of the molecular clock states that macromolecules should diverge from one another at a constant rate.

Biological Clock

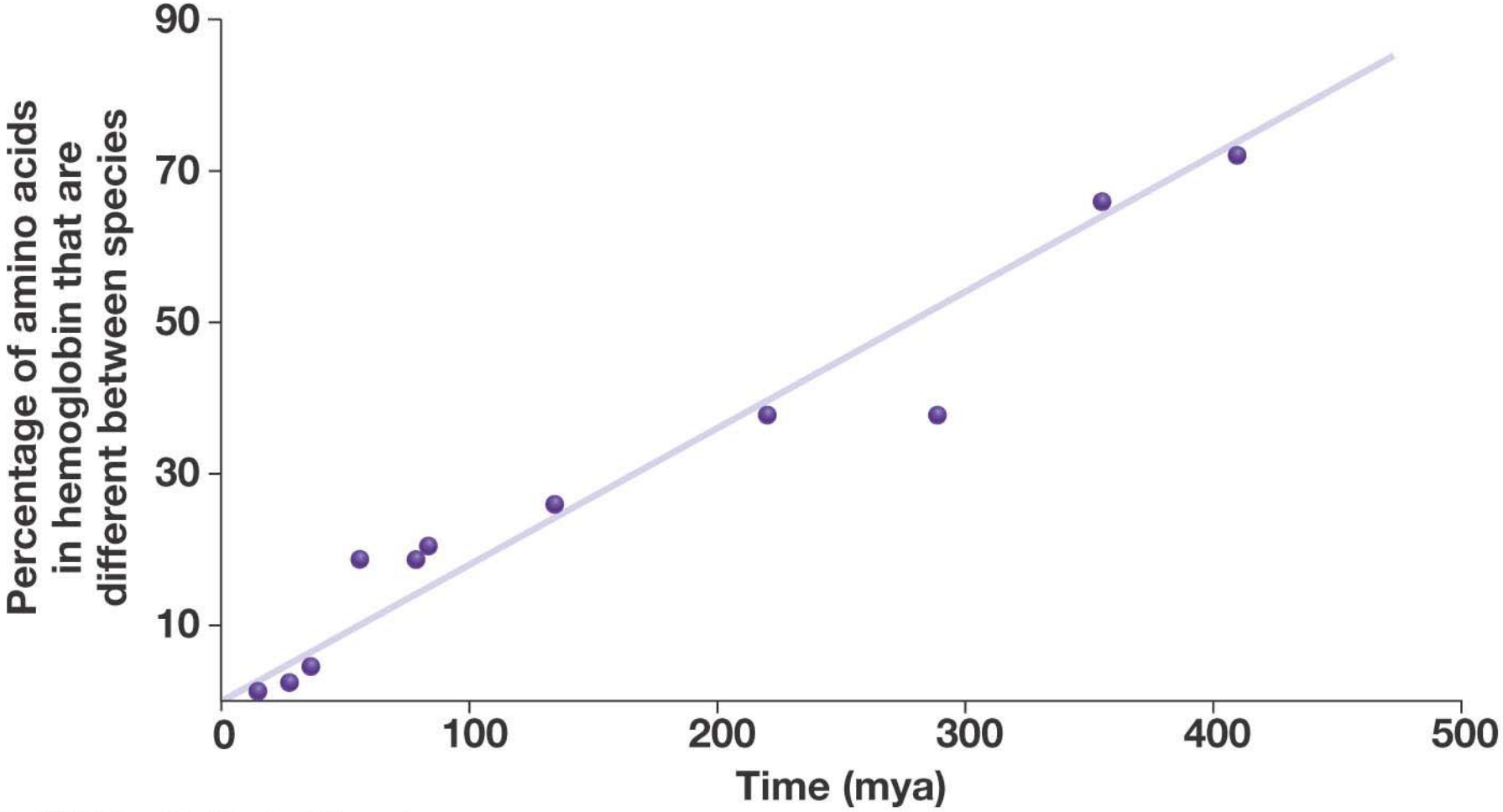
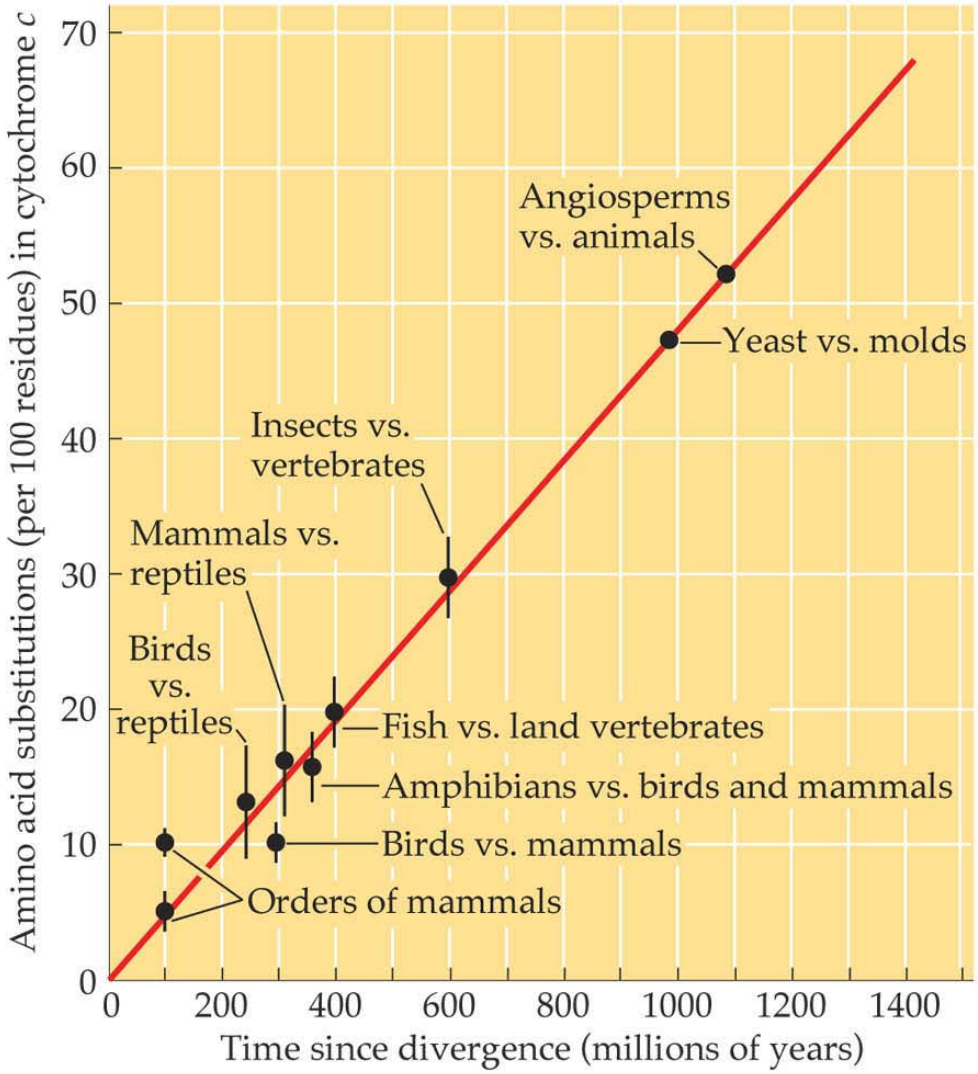


Figure 26.5 *Cytochrome c Has Evolved at a Constant Rate*

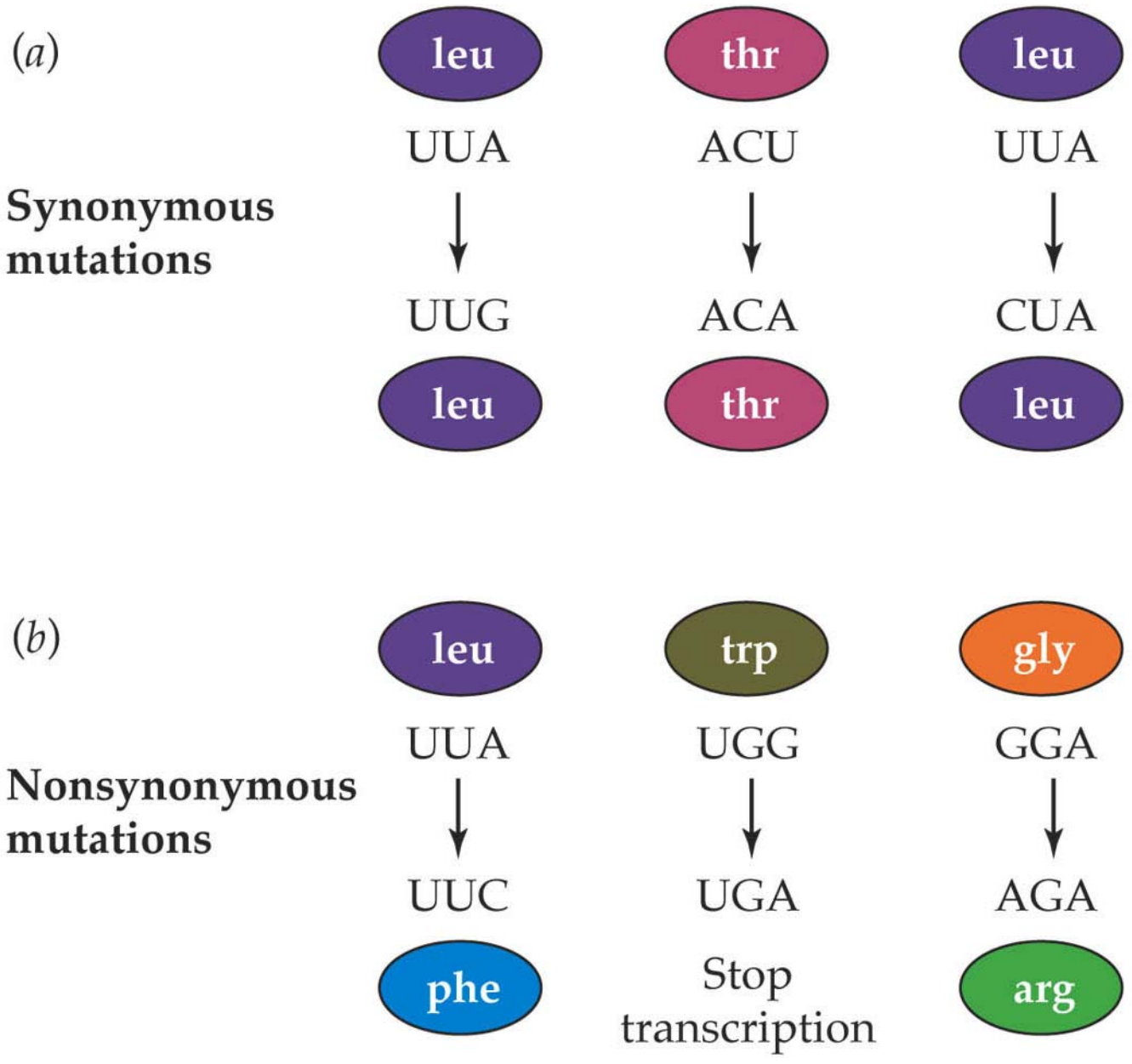


Cytochrome *c* sequences have evolved at a relatively constant rate.

The Evolution of Macromolecules

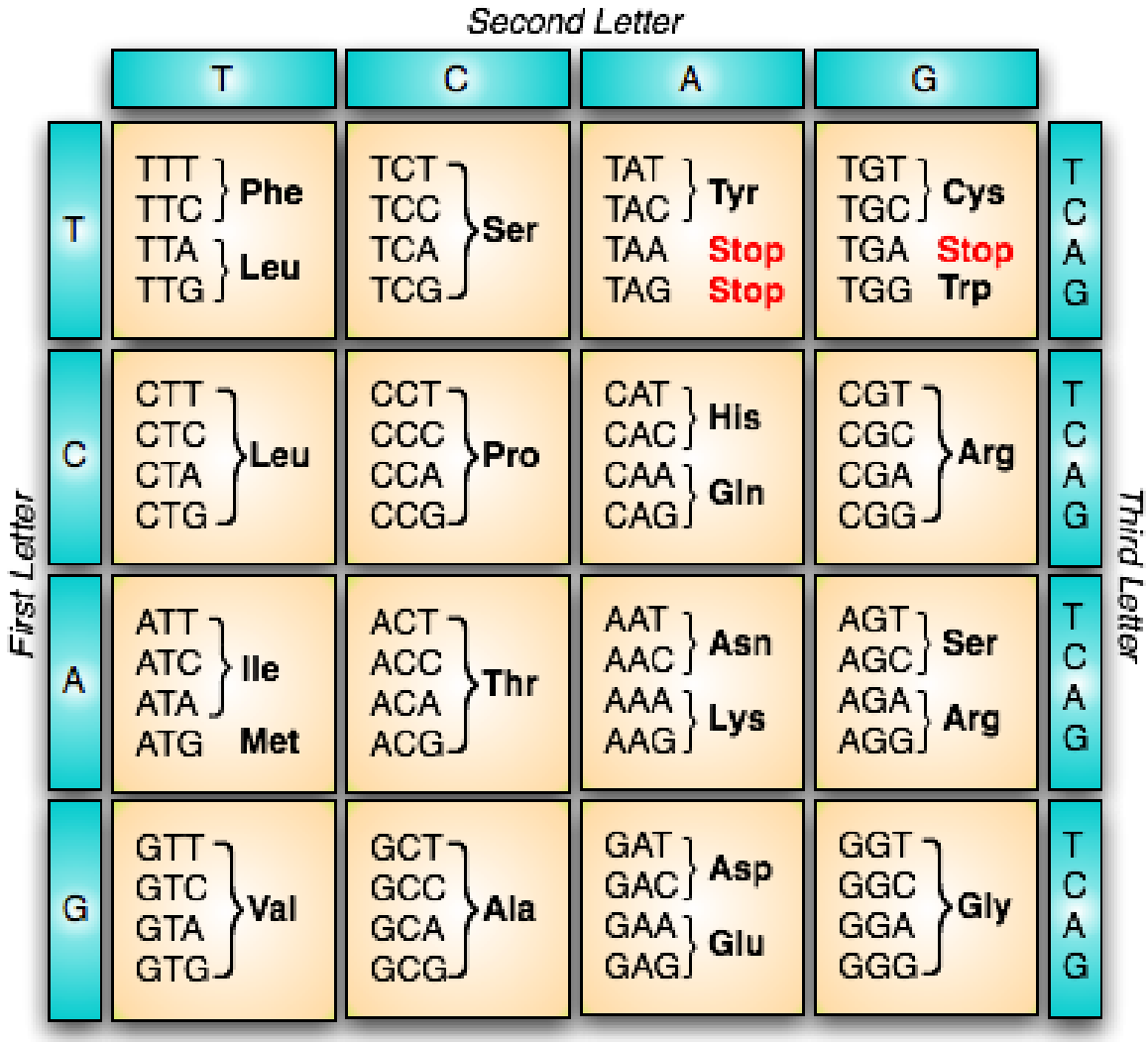
- Molecular evolution differs from phenotypic evolution in one important way:
  - In addition to natural selection, random genetic drift and mutation exert important influences on the rates and directions of molecular evolution.
  - What does this say about our study of "Evolutionary Theory"?
- Many mutations, called **silent** or **synonymous** mutations, do not alter the proteins they encode
- A **nonsynonymous mutation** does change the amino acid sequence

Figure 26.1 *When One Base Does or Doesn't Make a Difference*



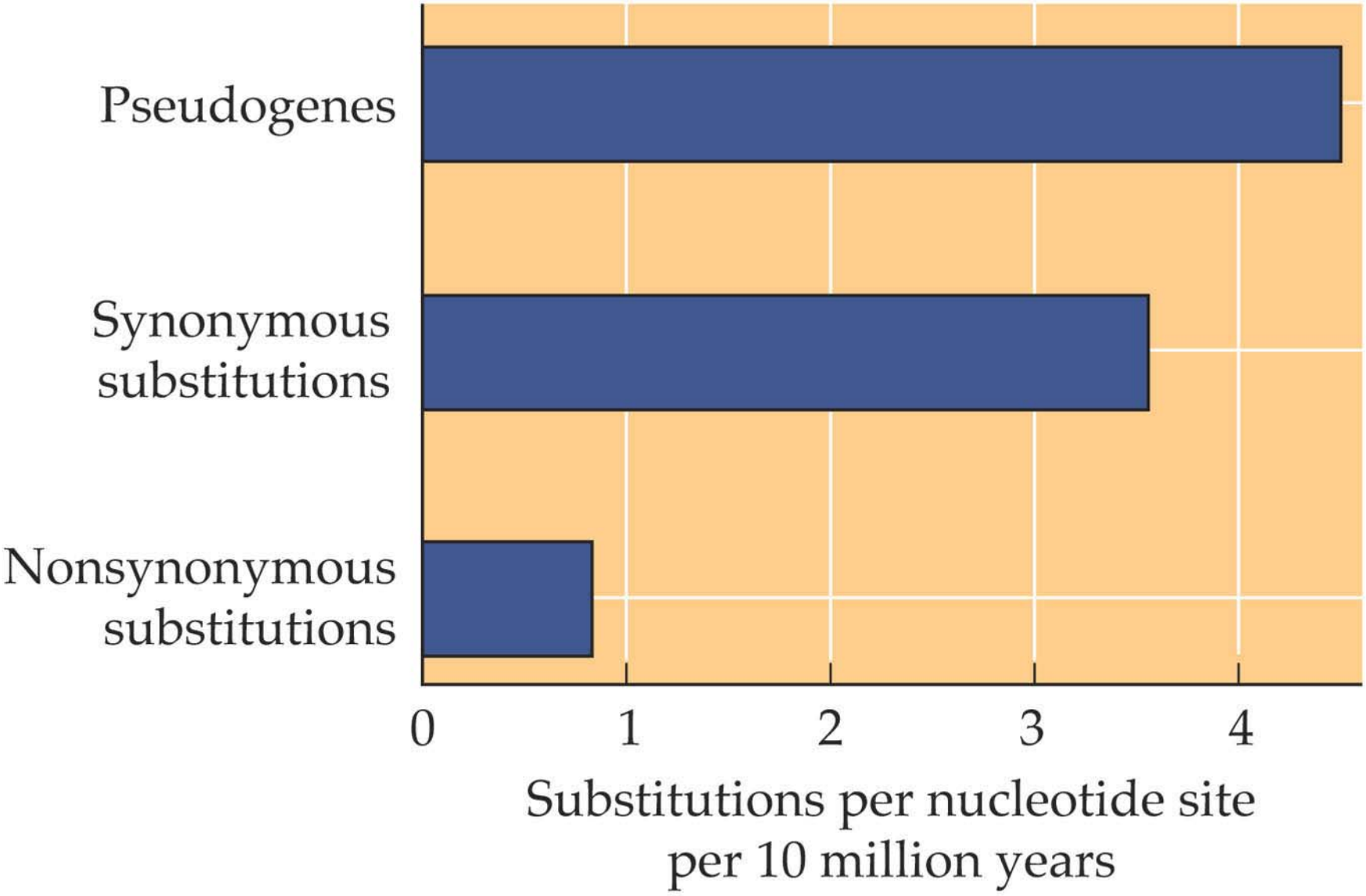
LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition, Figure 26.1 When One Base Does or Doesn't Make a Difference

Genetic Code (DNA → amino acid)



http://plato.stanford.edu/entries/information-biological/GeneticCode.png

Figure 26.3 *Rates of Base Substitution Differ*



LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition, Figure 26.3 Rates of Base Substitution Differ

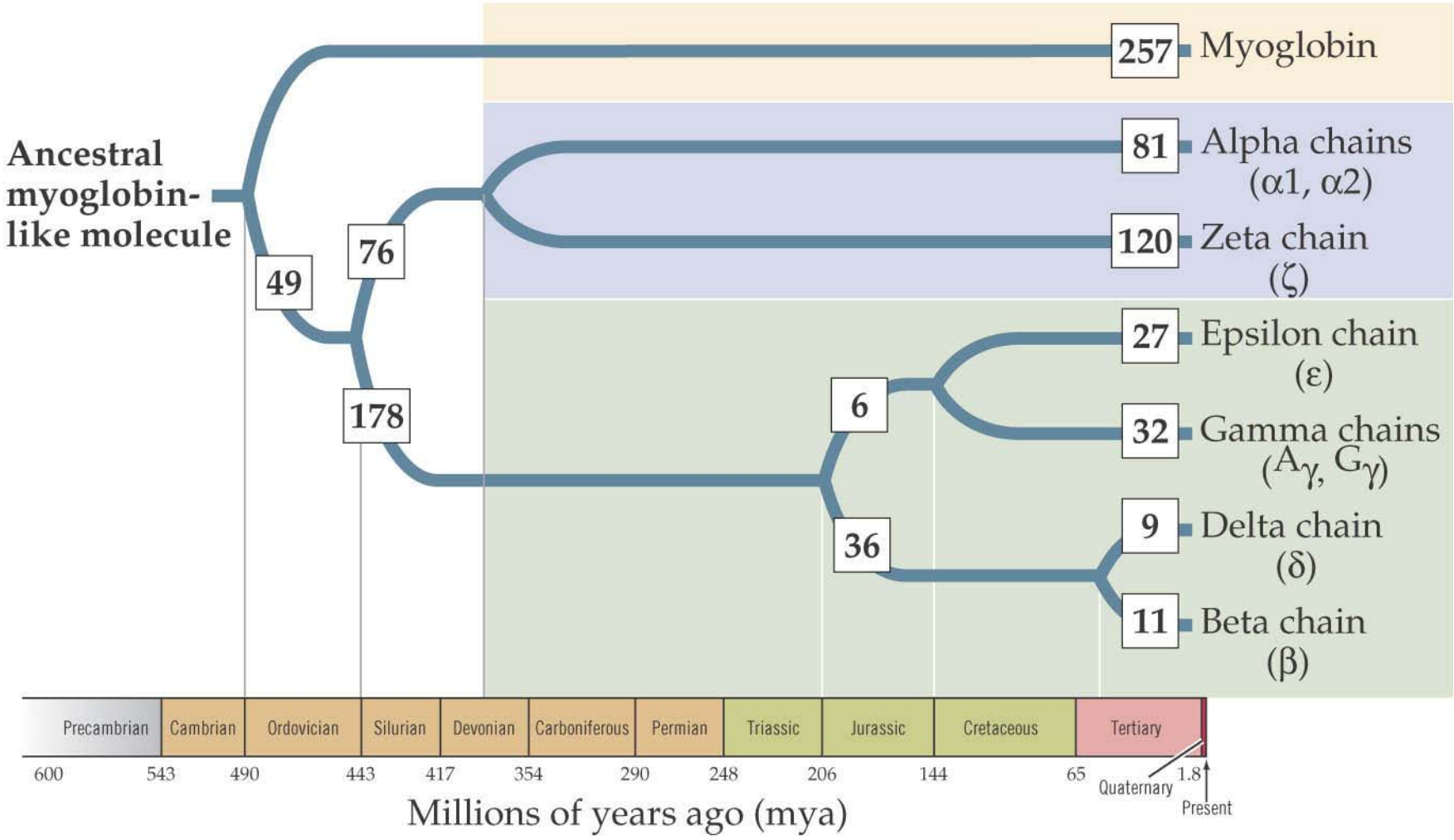
The Evolution of Genome Size

- Several rounds of duplication and mutation may lead to formation of a gene family, a group of homologous genes with related functions.
- There is evidence that the globin gene family arose by gene duplication.

  = Neofunctionalization

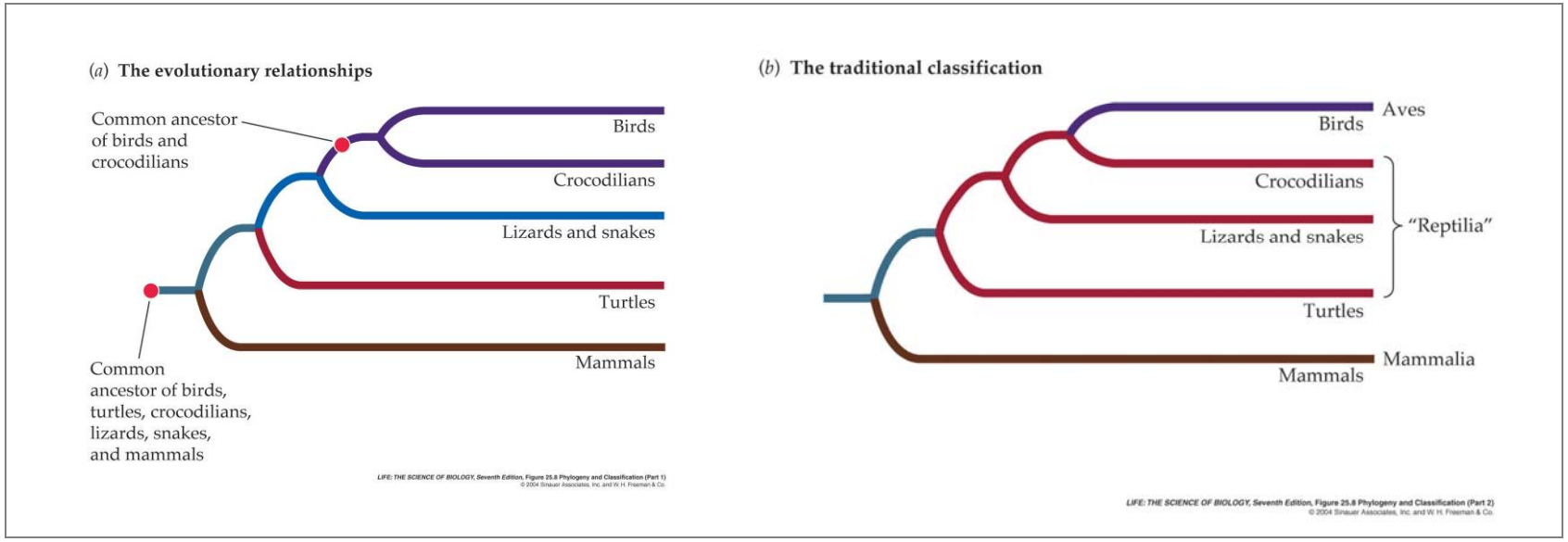
- To estimate the time of the first globin gene duplication, a **gene tree** can be created.
- Based on the gene tree, the two globin gene clusters are estimated to have split about 450 mya.

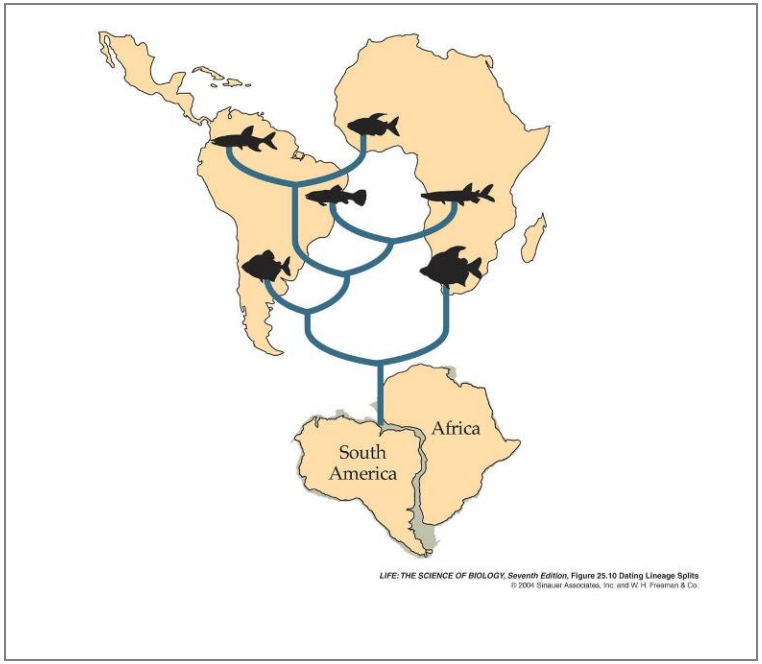
Figure 26.9 *A Globin Family Gene Tree*



***LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition,* Figure 26.9 A Globin Family Gene Tree**

Figure 25.8 *Phylogeny and Classification*





What are the major biological principles illustrated in these two examples?